AN ABSTRACT OF THE THESIS OF

Katherine M. Jacobs for the degree of Master of Science in Forest Science,
presented on April 30, 2002.
Title: Response of Small Mammal Mycophagy to Varying Levels and Patterns of
Green-tree Retention in Mature Forests of Western Oregon and Washington.

Abstract approved: _____

Daniel L. Luoma

The Demonstration of Ecosystem Management Options (DEMO) study is a

large-scale, multi-year, interdisciplinary project examining the effects of various

levels and patterns of green-tree retention on multiple forest features. Six retention

levels and patterns were examined and replicated across six blocks of

predominately Douglas-fir forested land in western Oregon and Washington. As

part of the DEMO study, this research focuses on the effects of these silviculture

activities on small mammal mycophagy. The diets of three small mammal groups

were examined: squirrels (the northern flying squirrel, *Glaucomys sabrinus*),

chipmunks (Townsend's chipmunk – *Tamias townsendii*, and the Siskiyou

chipmunk – *T. siskiyou*), and voles (the western and southern red-backed voles –

Clethrionomys californicus and *C. gapperi*). These animals are vital fungal spore

dispersers and forest prey. Fecal pellet analysis was used as a non-lethal method of

examining the diets of these mycophagous mammals. Fecal samples were

collected from these animals before and after the application of treatments. Pre-

treatment diet data was utilized for a diet comparison among the animal genera.

The change in the frequencies for the common truffle genera, plant material, and total cumulative number of genera were compared using an analysis of variance to measure the effect of each treatment on the diets of the study animals.

The pre-treatment fungal diets of the study animals showed significant differences among genera. *Glaucomys sabrinus* fecal samples contained higher frequencies of *Gautieria* and *Leucogaster* spores than either *Clethrionomys* or *Tamias* samples. The diet of the *Tamias* spp. contained higher frequencies of plant material than *G. sabrinus* or *Clethrionomys*, emphasizing the more diverse diet of this animal genus. *G. sabrinus* samples contained the highest mean number of truffle genera per sample and consistently contained a high frequency of the four common truffle genera. Moderately high frequencies of the common truffle genera were common in the *Clethrionomys* samples. Only the genus *Rhizopogon* was commonly found in high frequencies in the *Tamias* samples. The frequency of *Rhizopogon* spores was consistently greater than 95% in the pre-treatment diets of all animal genera.

Treatment effects were found for different diet items for each animal genus. The mean total cumulative number of truffle genera in the diet of the study animals showed little change. The harvesting of trees appears to negatively affect the frequency of *Rhizopogon* spores in the diet of *Clethrionomys,* potentially reflecting the reduced ability of these animals to forage for *Rhizopogon* truffles and a reduction in *Rhizopogon* truffle abundance or frequency, especially in the 15% aggregated retention treatment. The retention of trees in isolated aggregates

restricts the movement of *Clethrionomys* within the treatment and the abundance of edge on the aggregates may further restrict *Clethrionomys* to the center of the aggregates. Competition would be increased within these aggregates where animals are concentrated and the resource may be even more limited.

In the diet of *G. sabrinus*, the frequency of *Gautieria* spores significantly decreased in the 40% aggregated retention treatment and increased in the 40% dispersed retention treatment. The retention of trees in aggregates may limit the ability of *G. sabrinus* to move and forage between aggregates and into adjacent habitat. However, in the dispersed retention treatments, adequate travel routes are still available and *G. sabrinus* could forage throughout the treatment and in to adjacent habitat, thus reducing the impact of the reduction of truffle biomass within a stand.

The diet of the *Tamias* spp. showed little change in response to the treatments. The wide diversity of habitats that *Tamias* utilize may extend the ability of this animal to find and compete for truffles even as they decreased locally, until a large decrease in biomass occurred.

The sporocarp biomass data (D. Luoma, unpublished data) showed that overall truffle biomass declined, whereas consumption of truffles by these small mammals largely stayed the same. This suggests that the animals are compensating for a locally declining food source by altering their foraging behavior. The long term effects of this behavioral compensation on energetics and population dynamics is unknown.

Response of Small Mammal Mycophagy to Varying Levels and Patterns of Green-tree Retention in Mature Forests of Western Oregon and Washington.

by
Katherine M. Jacobs

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented April 30, 2002.
Commencement June 2003.

<u>Master of Science</u> thesis of <u>Katherine M. Jacobs</u> presented on <u>April 30, 2002</u>.

APPROVED:

_____

Major Professor, representing Forest Science

_____

Head of the Department of Forest Science

_____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

_____

Katherine M. Jacobs, Author

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

Response of Small Mammal Mycophagy to Varying Levels and Patterns of Green-tree Retention in Mature Forests of Western Oregon and Washington

INTRODUCTION

Historically, clearcutting has been considered a viable and economical way of harvesting timber from the predominately Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] forests of the Pacific Northwest (for more details see Aubry *et al.*, 1999; Halpern *et al.*, 1999). However, the complete removal of mature trees from large tracts of land and the use of heavy logging machinery can severely impact a forest ecosystem by drastically altering structural, habitat, and soil microsite conditions (Rogerson, 1976; Franklin and DeBell, 1979; Stark, 1979). As a result of clearcutting large tracts of land, some species may be locally extirpated or become isolated while populations of other species explode (SAF, 2002). If not carefully managed, forests that reestablish in clearcuts may contain fewer native and rare species whereas the number of exotic invasive species may increase (Halpern and Spies, 1995). Better understanding of these effects and public concern over the unsightliness of clearcuts (Ribe, 1999) has led to the use of alternative methods for harvesting timber that retain some of the structural and functional components of mature forests and mitigate forest disruption. In the Pacific Northwest, concerns about timber management practices and the loss of habitat for certain species led to the creation of the Northwest Forest Plan which set

specific guidelines for the management of federally-owned late-successional and old-growth forest related species within the range of the northern spotted owl (USDA and USDI, 1994).

Green-tree retention, the practice of leaving live, structurally-sound, large trees in a stand after extracting timber, is an alternative forest management method designed to accelerate the development of late-successional forest characteristics in young, managed stands (Aubry *et al.*, 1999). The Demonstration of Ecosystem Management Options (DEMO) project is a long-term study designed to examine the effects of different levels and patterns of green-tree retention on multiple forest attributes (see Aubry *et al.*, 1999). The research presented in this thesis is but one part of the DEMO study and focuses on an important aspect of mature forests, the complex interrelationships among trees, fungi, and animals in the Pacific Northwest (PNW): small mammal mycophagy.

In the PNW, ectomycorrhizal fungi (EMF) are an integral part of the forest ecosystem (Malajczuk *et al.*, 1987; Luoma, 1988; Maser *et al.*, 1988; Amaranthus *et al.*, 1994; Clarkson and Mills, 1994; Carey *et al.*, 1999). They are important for tree health and vigor and as a food source for animals (Trappe and Maser, 1977). A wide diversity of fungi are ectomycorrhizal; commonly, multiple fungi are capable of forming ectomycorrhizae with a single tree species (Trappe and Fogel, 1977; Smith and Read, 1997). For example, Trappe (1977) estimated that 2,000 fungal species form ectomycorrhizae with Douglas-fir alone.

Ectomycorrhizal fungi form a mutually beneficial relationship with the feeder roots of a variety of forest trees, including members of the Betulaceae, Fagaceae, and Pinaceae (Smith and Read, 1997). This relationship provides the heterotrophic fungi with photosynthates and increases the tree's water and nutrient uptake. Some EMF form hypogeous (underground) sporocarps, commonly known as truffles (ascomycetes) or false truffles (basidiomycetes). For convenience, all hypogeous sporocarps will be hereafter referred to as truffles. These sporocarps are an important belowground food source for many small mammals in the PNW (Trappe and Maser, 1977; Fogel and Trappe, 1978; Maser *et al.*, 1978; Rhoades, 1986; Amaranthus *et al.*, 1994; North *et al.*, 1997; Zabel and Waters, 1997). In turn, these mammals act as fungal spore dispersers, disseminating propagules throughout the forest and into non-forested habitat (Trappe and Maser, 1977; Fogel and Trappe, 1978). These mycophagous (fungus-eating) small mammals are important prey to many raptors and other predators, including the threatened northern spotted owl (*Strix occidentalis* ssp. *caurina*) (Forsman *et al.*, 1984). When humans manipulate forests for timber production and extraction, this vital web between mammal, fungus, and tree, as well as the predator-prey relationship, can be disrupted. Consequently, it is important to find ways to harvest timber while still maintaining mature forest legacies.

The research included in this thesis focuses on determining the effects of leaving live trees at varying proportions of the original stand volume and in varying spatial patterns on the consumption of truffles by certain small mammals. Three

small mammal groups were chosen for the study: squirrels, voles, and chipmunks. These animals are important fungal spore dispersers as well as important prey items to many raptors and mammals (Maser *et al.*, 1978; Trappe and Fogel, 1978; Hayes *et al.*, 1986; Maser and Maser, 1988a). The diets of the northern flying squirrel, the western red-backed vole and its counterpart in Washington, the southern red-backed vole, and two chipmunks, Townsend's and the Siskiyou chipmunk, were examined.

The general objective of this study was to determine which levels and patterns of green-tree retention maintained the fungal diets of these small mammals and which significantly changed the fungal diets of these small mammals from their pre-treatment condition. Specific objectives of the research were:

1) To document the diets of the study animals under the pre-treatment conditions.

2) To detect any diet changes associated with the treatments by comparing the pre- and post-treatment total cumulative number of genera and mean spore frequency of the most common truffle genera in the diets of the study animals.

It was hypothesized that:

1) The pre-treatment diets of the study animals will differ significantly among genera.

2) The total cumulative number of truffle genera in the diet of the study mammals will significantly change as a result of the harvesting of trees,

showing the most change in treatments with the least percentage of green-trees retained.

3) The mean frequencies of the most common truffle genera spores in the diets of these study animals will show a significant change in the treatment units. The diet of animals captured in treatments with less trees retained will show greater change than the diet of animals captured in treatments with higher green-tree retention levels.

LITERATURE REVIEW

TRUFFLES, TREES, AND SMALL MAMMALS

Fungi that produce truffles are an integral component of forests throughout the world (Trappe and Maser, 1977; Maser *et al.*, 1978; Lamont, *et al.*, 1985; Blaschke and Bäumler, 1989; Carey *et al.*, 1999). Nearly all known truffle species are thought to be ectomycorrhizal, forming a mutualistic relationship with the roots of trees and other plants (Smith and Read, 1997). The plant root tips are colonized by the hyphae of ectomycorrhizal fungi (EMF). The hyphae form a mantle around the root tip and penetrate in between the cells of the cortex layer of the root to form a network of hyphae called the Hartig net (Massicotte *et al.*, 1986; Massicotte *et al.*, 1990). Root tips may be colonized by one or multiple species of EMF (Trappe and Fogel, 1977). Hyphae from the fungal mantle extend into the soil, where they absorb nutrients, ions, and water which are then transferred to the associated plant. In addition to providing the host plant with nutrients and water extracted from the soil, EMF provide other benefits that improve the health of the host plant. For example, the fungal mantle can act as a barrier to root pathogens as well as increase the longevity of feeder roots (Marx, 1973; Trappe and Fogel, 1977; Duchesne, 1994). The heterotrophic EMF benefit by receiving photosynthates from the host plant (Alexopoulous *et al.*, 1996). The plants and fungi are highly reliant on one another and many ectomycorrhizal relationships have become obligatory (Trappe and Luoma, 1992; Smith and Read, 1997).

According to Trappe and Fogel (1977) "most woody plants need mycorrhizae to survive, and most herbaceous plants need them to thrive." In laboratory conditions, plants in mycorrhizal associations have shown growth and health advantages over non-mycorrhizal plants. *Eucalyptus* seedlings from Australia grown in soil inoculated with *Mesophellia* spores had a higher mean shoot dry weight than non-mycorrhizal seedlings grown in spore-free soil (Ashton, 1976). The plant *Leptospermum scoparium* from New Zealand showed a positive growth response when the surrounding soil was inoculated with Endogonaceae spores (Cooper, 1975). The plants studied by Cooper (1975) showed a dependence on mycorrhizae when grown in soil with limited available phosphorus. The growth of citrus tree seedlings planted in inoculated and non-inoculated soil was studied by Kleinschmidt and Gerdemann (1972). Seedlings without endomycorrhizae became stunted and did not grow as well as those that were able to form mycorrhizae. These experiments and many more have shown that the formation of mycorrhizae confers growth benefits to many woody and herbaceous plants (Smith and Read, 1997).

Most known ectomycorrhizal fungi produce either truffles or aboveground (epigeous) mushrooms for sexual reproduction. In general, truffles range in size from a few millimeters to several centimeters in diameter (Castellano *et al.*, 1989). In the PNW, most truffles can be found in the top 10 cm of the soil surface, near the organic soil-mineral soil interface (Luoma *et al.*, 1991). This thin layer of soil

helps to protect truffles from desiccation and freezing. As a result, the optimal fruiting time is lengthened relative to epigeous mushrooms (Thiers, 1984).

The spore-producing structures of most truffles are enclosed in an outer layer of sterile tissue called the peridium. The enclosed nature of the spore-bearing tissues and fruiting underground prevents truffles from readily dispersing spores by means of air or water. Although the peridium may decompose in the soil, exposing spores, the spores will only be dispersed in the immediate vicinity (Miller *et al.*, 1994). Truffles rely upon small mammals to adequately disperse their spores. The relationship between small mammals and truffles has evolved over time, resulting in mycophagous mammals exhibiting particular "food-gathering behavior" that enables them to locate fungi (Fogel and Trappe, 1978; Pyare and Longland, 2001a).

As truffles mature, they produce strong, chemically complex odors that attract many small mammals (Trappe and Maser, 1977; Donaldson and Stoddart, 1994). The scent a truffle exudes may contain chemical compounds similar to certain animal hormones. Human male and female participants in a truffle odor trial responded differently to the scents (Marin and McDaniel, 1987). Responding to these olfactory cues, small mammals are extremely adept at uncovering mature sporocarps (Donaldson and Stoddart, 1994; Pyare and Longland, 2001a). As an animal consumes the truffle, many fungal spores are ingested; these spores remain viable after passage through the animal's digestive tract (Trappe and Maser, 1976; Kotter and Farentinos, 1984). Moreover, studies suggest that the spores of some truffle species may require passage through an animal's digestive tract before they

will germinate (Lamont *et al.*, 1985; Claridge *et al.*, 1992). For example, spores obtained directly from sporocarps of the Australian truffle, *Mesophellia pachythrix*, applied to the soil around eucalyptus trees did not form ectomycorrhizae whereas *M. pachythrix* spores that came from fecal pellets did. In this case, it was not determined whether passage through the gut or some other factor allowed the spores to germinate in natural forest soil conditions (Claridge *et al.*, 1992).

As mycophagous mammals travel and defecate, viable truffle spores are dispersed throughout the forest. These spores are washed into the soil by precipitation and mechanical action and are available to form ectomycorrhizae on new roots (Claridge *et al.*, 1992; Miller *et al.*, 1994). Tunneling animals that defecate near tree roots also serve to spread fungal spores. Animal dispersal of fungal spores can serve to increase local genetic diversity of the fungi as well as introduce new fungi to an area (Maser *et al.*, 1978; Miller *et al.*, 1994).

Just as truffles are found around the world, so are mycophagous mammals. Evidence from Australia (Lamont, *et al.*, 1985; Claridge and Lindenmayer, 1998), Europe (Hastings and Mottram, 1916; Blaschke and Bäumler, 1989), Argentina (Perez Calvo *et al.*, 1989) and North America (Trappe and Fogel, 1977; Trappe and Maser, 1977; Amaranthus *et al.*, 1994; Cázares and Trappe, 1994) suggests that mycophagy is widespread and important for the health of forests. In the PNW, many small mammals strongly depend upon truffles for a large part of their diets throughout the year (Maser *et al.*, 1978; Maser and Maser, 1988a). Elevation and habitat influence the diversity of truffles eaten by animals and the degree to which

animals rely on fungi as dietary items (Ure and Maser, 1982; Maser and Maser, 1988b; North *et al.*, 1997). Truffle production is dependent upon temperature and moisture conditions (Fogel, 1976). Thus, the species mix and biomass of truffles that is available for animal consumption varies yearly and seasonally (Luoma, 1991; Luoma *et al.*, 1991).

NUTRITIONAL VALUE OF TRUFFLES

Although several studies have provided knowledge on the nutritional value of truffles to mammals, much remains to be learned. Truffles are largely composed of water, suggesting that relatively large quantities must be eaten to gain adequate nutrition (Miller and Halls, 1969). However, truffles contain substantially greater amounts of nitrogen, phosphorous, potassium, sodium, iron, and aluminum than some mushrooms (Fogel, 1976; Grönwall and Pehrson, 1984). Truffles may also contain higher concentrations of these elements than some plants; levels of phosphorous and zinc are 20 to 50 times higher in sporocarps than in most plants eaten by herbivores (Stark, 1972). Fungi also contain vitamins (Shemakhanova, 1967), nonmetallic and metallic elements (Stark, 1972), steroids, triterpenes, amines, indoles, and phenols (Catalfamo and Trappe, 1970) that could potentially benefit mycophagous animals.

Chemical analysis of *Rhizopogon vinicolor*, a common fungus in western North America (Luoma *et al.*, 1991; States and Gaud, 1997; Carey *et al.*, 2002), demonstrated that, although the concentration of nitrogen and potential energy was

high, most of it was in an indigestible form (Claridge *et al.*, 1999). Western red-backed voles fed only *R. vinicolor* truffles in a controlled feeding experiment decreased slightly in body mass. This result led the researchers to conclude that a single species diet of *R. vinicolor* truffles was "only of moderate nutritional value for most small, hindgut-fermenting mammals" (Claridge *et al.*, 1999). Examination of the nutritional value of *Elaphomyces granulatus* truffles for the golden-mantled ground squirrel (*Spermophilus saturatus*) showed that nitrogen in this truffle was also largely bound in indigestible compounds (Cork and Kenagy, 1989). The researchers concluded that, under their experimental conditions, *E. granulatus* was not a high-quality dietary item. They speculated that the dietary value of this truffle is derived from its great abundance and availability for consumption (Cork and Kenagy, 1989).

Dubbed the "fast food of the forest" by Bennett and Byrony (1997) for their abundance and attractiveness to squirrels, truffles have nutritional value because they are readily available and highly detectable by small mammals - thus reducing the energy cost of foraging (Trappe and Maser, 1977; Fogel and Trappe, 1978; Cork and Kenagy, 1989; Claridge *et al.*, 1999; Pyare and Longland, 2001a). For example, Smith (1968) demonstrated that for red squirrels, consuming fungi is energetically more efficient than eating conifer seeds - providing a much larger energy intake per unit feeding time than lodgepole pine seeds.

The nutrition an animal obtains from eating truffles varies among species, especially those with different gut structures. Despite evidence that truffles have

only moderate nutritive value, the body condition of Australian potoroid marsupials appears to improve with increasing amounts of fungus in the diet. These animals have a foregut, which may aid in the breakdown of fungal material (Johnson, 1994). Animals lacking foreguts may obtain additional nutrients from truffles by caecotrophy (Johnson, 1994).

THE EFFECTS OF FOREST MANAGEMENT ON ECTOMYCORRHIZAL FUNGI

Managed versus unmanaged forests

Not only do managed and unmanaged stands tend to differ visibly aboveground, but management prescriptions markedly affect the belowground community as well. Young stands may have a different composition of truffle species than unmanaged mature or old-growth stands (Luoma, 1988 and 1991). Smith *et al.* (2002) examined the hypogeous and epigeous sporocarps produced in unmanaged old-growth versus managed rotation-age and young stands in the Cascades of Oregon. They found that 36% of the sporocarps examined were unique to an age class. Studies have shown that truffle species richness, annual production, and standing crop tend to be higher in older unmanaged stands than in young managed ones (Vogt *et al.*, 1981; North *et al.*, 1997). Additionally, the dominant truffle species in these stand types differ (North *et al.*, 1997, Smith *et al.*, 2002). In contrast to earlier studies, Smith *et al.* (2002) found that truffles were

found more frequently in young and rotation-age stands than in old-growth stands, and that the younger stands produced three times more sporocarp biomass (truffles and mushrooms) than the old-growth stands. Since Smith *et al.* (2002) was a retrospective study, the change in truffle production in the managed stands versus their pre-cutting condition is unknown. Despite differences among studies, these results suggest that during forest succession, the diversity, abundance, and composition of EMF change. The truffle community in stands that have been altered by management prescriptions differs markedly from that in unmanaged stands in the Pacific Northwest (North *et al.*, 1997).

Clearcutting

The roots of trees provide the habitat for EMF; therefore, the presence of EMF and the production of truffles are closely linked to the host trees. When the trees are removed or the composition of trees in a stand changes, species richness or the composition and abundance of truffles in the stand changes as well (Amaranthus *et al.*, 1994; Clarkson and Mills, 1994; Waters *et al.*, 1994; North *et al.*, 1997; Colgan *et al.*, 1999). Clearcutting is especially detrimental to EMF diversity and abundance, as all potential hosts are removed. The removal of the host tree essentially cuts off the supply of carbon to the fungus and prevents it from producing sporocarps (Amaranthus *et al.*, 1994). Additionally, soil compaction or changes in soil temperature and moisture regimes will heavily impact the production of truffles (Waters *et al.*, 1994; Cázares *et al.*, 1998).

A positive relationship between truffle production and the presence of coarse woody debris (CWD) has been suggested by several researchers (Luoma, 1988; Luoma *et al*, 1991; Amaranthus *et al.*, 1994). Many forest management practices impact the amount and decay class of CWD in a stand (Harmon *et al.*, 1986). This too, may affect truffle production, abundance, or diversity. Older forests tend to have more CWD in the later stages of decomposition than younger or recently clearcut stands (Harmon *et al.*, 1986).

The number of sporocarps produced in late-seral forests may greatly outnumber those produced in plantations regenerated from clearcuts. Late-seral forest remnants in southwestern Oregon had twenty to forty times more sporocarps than the surrounding 10-27 year-old plantations developed from clearcuts (Clarkson and Mills, 1994). Only one truffle was found in the eighty sample plots placed within the 10-27 year-old plantations. Within the late-seral stands, truffles were four times more numerous in plots with CWD than without (Clarkson and Mills, 1994).

Amaranthus *et al.* (1994) compared the numbers of truffles and truffle dry weight between 180 year-old mature Douglas-fir forest fragments and the 4 to 27 year-old plantations surrounding them. A positive association between stand age, amount of CWD, and truffle production was evident. A greater number, diversity, and total dry weight of truffles were found in the mature stands than in the plantations. Thirteen of the twenty-one truffle species recorded in that study were found only in the mature stands and eight species were found only under CWD.

The effect of CWD on truffle production was only evident in the mature stands. In the mature forest fragments, there were more truffles and greater truffle biomass associated with CWD as compared to soil (Amaranthus *et al.*, 1994). Since highly decayed CWD retains water, truffles may be produced under CWD even in times of drought. The retention of mature forest fragments in the managed landscape provides a more diverse food source for small mammals during critical times, such as periods of drought, than would be available in younger stands (Amaranthus *et al.*, 1994).

Thinning

Thinning is a common silvicultural practice throughout the world (SAFnet, 2002). Unlike clearcutting, thinning retains residual trees that can act as refuges for EMF. However, studies indicate that thinning affects the composition and diversity of EMF in the stand as well as the frequency of sporocarps (Waters *et al.*, 1994; Colgan *et al.*, 1999; Carey *et al.*, 2002). For example, stands that are heavily thinned may show an increased dominance by one fungal species (Colgan *et al.*, 1999). Thinning also reduces truffle biomass, reduces the frequency of sporocarps, and shifts species dominance (Colgan *et al.*, 1999). A shift in truffle species composition in the stand can impact mycophagous animals by altering the nutritional balance of their diets (Gurnell, 1987; Carey *et al.*, 1999).

Green-tree retention

The retention of green trees in a manipulated stand can moderate the impact of host loss by acting as a refuge for EMF diversity. Stockdale (2000) examined ectomycorrhizal root tips within the area beneath the crown of retained trees and in open areas removed from hosts. Ectomycorrhizal fungus richness was highest under the crown and declined further from the tree, with diversity being lowest in the open areas. EMF richness was reduced by as much as 50% in open areas compared to within the dripline of a tree. Species composition also differed between open areas and areas within the dripline. Stockdale's (2000) study provides evidence that green trees act as refuges for legacy species and are important in maintaining EMF diversity in managed stands.

Summary

Many of the studies reviewed above documented a shift in truffle species composition, diversity, and dominance in managed stands as compared to unmanaged ones (Vogt *et al.*, 1981; Amaranthus *et al.*, 1994; Clarkson and Mills, 1994; Waters *et al.*, 1994; North *et al.*, 1997). Some studies also found a difference in biomass and sporocarp frequency between managed and unmanaged stands. Taken as a whole, these studies indicate that forest management practices have a profound effect on truffle communities. Forest management practices that drastically alter local EMF populations create effects that may resonate throughout the tightly knit relationship between trees, truffles, small mammals, and predators.

EFFECTS OF SILVICULTURAL PRACTICES ON MYCOPHAGY AND SPORE DISPERSAL

As the diversity, composition, and abundance of truffles in a forest change, the ability of small mammals to find an adequate amount and diversity of food may be affected. This, in turn, may affect small mammal population numbers or species composition. Pyare and Longland (2001b) suggested that different small mammal species may disperse fungal spores in "ecologically nonredundant ways". Hence, a change in the small mammal population composition may influence fungal dispersal patterns.

Evidence also suggests that small mammals of different species compete with each other for the truffle food base (Pyare and Longland, 2001b). As truffle abundance and species diversity is reduced, those animals heavily reliant upon fungi for their diet may have difficulty finding adequate amounts of fungi. If small mammal abundances decrease, predators dependent on small mammals as prey may be impacted (Pyare and Longland, 2001b). During periods of low truffle production or when other food sources are not available, the reduction in truffle biomass due to the impacts of clearcutting and heavy thinning may have cumulative effects that extend to affect small mammal populations at a landscape scale.

STUDY ANIMALS

Clethrionomys californicus - Western red-backed vole

The western red-backed vole is found in western Oregon and northern California. This small mammal inhabits forested areas and is most common in closed-canopy old-growth forests with high levels of coarse woody debris (Maser and Maser, 1988b). Home ranges of males have been estimated at 0.74 ha and of females at 0.13 ha (Thompson, 1996). *C. californicus* is largely nocturnal and semifossorial (partially living under the ground). When aboveground, *C. californicus* rarely ventures far from CWD, which it uses for protection and cover (Foresman, 2001). The importance of CWD and litter depth for *C. californicus* increases in highly managed landscapes (Rosenberg *et al.*, 1994; Bowman *et al.*, 2000). Strongly mycophagous, the diet of *C. californicus* consists largely of truffles supplemented by lichens (Ure and Maser, 1982; Hayes *et al.*, 1986; Thompson, 1996). In one study, truffles composed a mean 85% (maximum 98%) of the stomach contents of *C. californicus* (Ure and Maser, 1982). Nineteen truffle genera have been identified in the fecal pellets of *C. californicus* in southern Oregon (Hayes *et al.*, 1986). Due to its reliance on a fungal diet, *C. californicus* is an important disperser of truffle spores in the forest (Thompson, 1996).

C. californicus is affected by clearcutting and forest fragmentation. A strong negative edge effect has been shown both for *C. californicus* population numbers and truffle production, suggesting that truffle distribution in forest

remnants may be one of the factors limiting *C. californicus* populations (Mills, 1995). *C. californicus* is rarely found in clearcuts and intensively logged areas will be nearly devoid of *C. californicus* until the canopy begins to close (Gashwiler, 1970; Ure and Maser, 1982). As a result, *C. californicus* infrequently disperses spores into severely disturbed areas.

C. californicus is an important part of the prey base in Pacific Northwest forests. Most notable among their predators is the northern spotted owl (Foresman, 2001). Martens, ermines, weasels, and skunks also prey upon *C. californicus* (Alexander and Verts, 1992).

Clethrionomys gapperi - Southern red-backed vole

The southern red-backed vole is similar in habitat and biology to the western red-backed vole. In the PNW, the range of this animal does not extend south of the Columbia River. Within Washington, *C. gapperi* is an important prey item for the northern spotted owl (Forsman *et al.*, 2001). *C. gapperi* is heavily affected by disturbance, and populations tend to decline following logging activities (Gashwiler, 1967; Sullivan *et al.*, 1999). In southern New England, a study demonstrated that *C. gapperi* has high kidney requirements for water and that *C. gapperi* must live in an area with "sufficient water or succulent food items" (Getz, 1968). Truffles, which are high in water content (Miller and Halls, 1969), could potentially fulfill this role.

Although both *C. californicus* and *C. gapperi* are mycophagous, their diets differ according to their habitat. While *C. gapperi* captured in the lowlands of Washington ate as much fungi as *C. californicus*, *C. gapperi* found in higher elevations in Washington had a higher incidence of conifer seeds in their stomachs (Ure and Maser, 1982). These observations led Ure and Maser (1982) to conclude that mycophagy for these voles is closely related to habitat conditions and not a feature specific to the species.

The conclusion that *Clethrionomys* consume truffles in relation to their availability in a particular habitat was further supported by Maser and Maser (1988b). They examined the stomach contents of *C. californicus* from western Oregon and *C. gapperi* from various areas across North America. In this study as well, habitat highly influenced the mycophagy of *C. gapperi*, suggesting a facultative aspect to its mycophagy. From the Rocky Mountains westward, 23 different fungal genera were observed in the diets of *C. gapperi*, but only 7 genera were recorded from animals further east. In comparison, *C. californicus* captured in Oregon consumed 28 fungal genera (Maser and Maser, 1988b). In light of these studies, *C. californicus* and *C. gapperi* seem to function equivalently as avid, yet facultative, mycophagists.

Glaucomys sabrinus - Northern flying squirrel

The northern flying squirrel is probably the most important prey species for the northern spotted owl across most of the owl's range with the exception of the

Klamath Province in northern California and southwest Oregon (Wells-Gosling, 1985; Zabel *et al.*, 1995; Colgan III *et al.*, 1997). In Washington, 29-54% of the northern spotted owl's prey base consisted of *G. sabrinus*, accounting for 45-59% of the prey biomass ingested (Forsman *et al.*, 2001). The importance of *G. sabrinus* in the diet of the northern spotted owl increases during the cold season. Many small mammals hibernate or become less active (undergo torpor) during winter. However, the northern flying squirrel continues to be active and available for predators (Foresman, 2001). During this time, *G. sabrinus* may compose 72% of the northern spotted owl's diet (Rosenberg, 1990). It is estimated that one pair of owls may consume up to 500 squirrels annually (Wells-Gosling, 1985).

The northern flying squirrel is widely distributed throughout the United States and Canada, inhabiting both coniferous and deciduous forests (Hall, 1981). Though an important factor, stand age class alone may not determine *G. sabrinus* abundance. Some research has shown that the northern flying squirrel is most abundant in old-growth coniferous forests of the Pacific Northwest (Carey *et al.*, 1999), whereas other research in the PNW provides evidence that squirrel densities were relatively equal between second- and old-growth forests (Rosenberg and Anthony, 1992). Research has also shown that the average home range of flying squirrels in old- and second-growth are equal (Martin and Anthony, 1999). These studies suggest that *G. sabrinus* is more of a generalist concerning stand age (Rosenberg and Anthony, 1992; Martin and Anthony, 1999). Although it is true that *G. sabrinus* can be found in a variety of stand age classes, the habitat

requirements (i.e. large snags for nesting sites, trees tall enough for glide) for this animal may not be met by all stand age classes. *G. sabrinus* is nocturnal and nests in the cavities of trees and snags (Wells-Gosling, 1985). It is popularly known for its flying leaps from tree to tree with legs outspread (Taylor, 2000).

The northern flying squirrel feeds primarily on truffles and lichens (McKeever, 1960). As a result of its food preferences, *G. sabrinus* spends a considerable amount of time on the ground foraging for fungi (Wells-Gosling and Heaney, 1984; Maser *et al.*, 1985). Since fungal spores may be retained in the gut of this animal up to 11 days, wide dispersal of spores is possible (Pyare and Longland, 2001b). As much as 90 percent of the material in the digestive tract of *G. sabrinus* has been found to be fungal material or lichens (Maser *et al.*, 1985). Maser *et al.* (1986) found that the diet composition of *G. sabrinus* tended to parallel the seasonal availability of sporocarps and suggested that, in general, it has no preference for a particular truffle species under those field conditions. A notable exception was the consumption of *Rhizopogon* sporocarps, which did not change with seasonal abundance (Maser *et al.*, 1986). This may have been an artifact of sample technique or an actual disproportional consumption of *Rhizopogon* by *G. sabrinus*. Subsequent food trial studies under laboratory conditions showed that *G. sabrinus* does have a preference for consuming certain species of truffles over others (Zabel and Waters, 1997). *Glaucomys sabrinus* were offered sporocarps, a lichen, and seeds under laboratory conditions. The truffles *Gautieria monticola* and *Alpova trappei,* and the lichen *Bryoria fremontii* were the top ranked food

items in the diet of the *G. sabrinus* in this food trial. *Rhizopogon* truffles, which are commonly consumed by many small mammals, were not included in the experiment (Zabel and Waters, 1997*).

Glaucomys sabrinus utilizes a wide range of forest habitats and has a home range of 3 to 6 hectares (Witt, 1992; Martin, 1994; Martin and Anthony, 1999). Therefore, management practices that cause small local reductions in fungal diversity and abundance may affect *G. sabrinus* less than animals with smaller home ranges (Gurnell, 1987). For example, thinning treatments applied to young stands (35-45 yrs. old) showed no strong effect on *G. sabrinus* density, but *G. sabrinus* density showed high positive correlation with biomass and frequency of hypogeous sporocarps (Gomez *et al.*, unpublished data in Smith *et al.*, 2002).

Although thinning a stand may not reduce *G. sabrinus* density, the removal of all trees from a large plot of land may affect the behavior of *G. sabrinus* as it is unlikely to travel across large areas devoid of trees (C. Maguire, pers. comm.). Since both diversity and abundance of truffles are important in the diet of *G. sabrinus* (Carey *et al.*, 1999), a combination of the negative effects of timber harvesting on truffle production and the loss of travel corridors may negatively impact this animal by limiting the abundance of, and access to, different species of truffles.

Tamias townsendii - Townsend's chipmunk

Townsend's chipmunk is found throughout western Oregon and Washington. The average home range of *T. townsendii* is approximately 0.1 hectares for females and 0.7 hectares for males (Carey, 1991). Although not known as a prey item for the northern spotted owl, it is eaten by many other birds and mammals (Rosenberg, 1990).

Tamias townsendii is primarily a diurnal species with a diet consisting of a more diverse array of food sources than either *Clethrionomys californicus* or *Glaucomys sabrinus* (Sutton, 1993). However, this chipmunk has been described as an "avid mycophagist" (Maser *et al.*, 1978). Tevis (1953) examined the stomach contents of *T. townsendii* from forests of the northern Sierra Nevada and found a high percentage of fungi in the diet throughout the year, though consumption peaked in fall. Foresters have typically regarded chipmunks as an impediment to reforestation, due to their appetite for tree seeds. However, their role as a disperser of fungal spores is important to the development of forest ecosystems (Maser *et al.*, 1978).

T. townsendii has been found in both mesic closed-canopy forests and clearcuts (Sutton, 1993). In the Oregon Coast Range, and likely elsewhere in Oregon, *T. townsendii* occupies a range of stand ages and successional stages (Hayes *et al.*, 1995). In one habitat preference study, *T. townsendii* was collected almost exclusively in clearcuts with heavy brush, and higher densities of brush were correlated with higher numbers of chipmunks (Horn and Babb, 1983). This

suggests that *T. townsendii* may be an important disperser of fungal spores into open areas (Trappe and Maser, 1977; Rosenberg, 1990). *T. townsendii* is one of the relatively few mycophagous small mammals that travels between forests and clearcuts. Maser *et al.* (1978) considered *T. townsendii* "the most important diurnal vector of [truffle] spores in western Oregon."

Tamias siskiyou - Siskiyou chipmunk

Tamias siskiyou occurs in several southern Oregon counties and in northwestern California (Hall, 1981). The Siskiyou chipmunk is also highly mycophagous. Sixteen different genera of truffles have been found in its stomach contents, and 96-99% of the stomachs examined contained truffle spores (McIntire, 1984). The ecology, biology, and habitat of *T. siskiyou* are similar to that of *T. townsendii*. With respect to mycophagy, *T. siskiyou* may be considered an ecological equivalent of *T. townsendii*.

SUMMARY

Mycophagous small mammals play important roles in coniferous forests of the Pacific Northwest. Not only do they disperse spores of EMF that are important to the health of the forest, but they also serve as prey for many raptors and carnivores. Several of the small mammals reviewed here are known prey of the threatened northern spotted owl. Forest management practices that alter the diversity and abundance of truffles and mushrooms in a forest may affect the

abundance and composition of prey species. Forest management decisions should take into account the importance of small mammals as fungal spore dispersers and as prey for other species.

Although a few studies have examined the effects of thinning on small mammal populations, none have examined the relationships among the EMF community, truffle production, mycophagy, and small mammal populations experimentally on such a large scale and over such a wide geographic area as the DEMO study. The DEMO study also benefits from being a long-term study. Baseline data were collected over several years prior to the application of treatments, and data will continue to be collected for many years afterwards. This research will be the first to examine the EMF community, sporocarp production, mycophagy, and the change in small mammal populations concurrently in response to silviculture treatments. Only by looking at these components of the forest together can we obtain the synthesis necessary to understand the impact of land management on forest health.

METHODS

The DEMO study is a complete randomized block study designed to examine the effects of different levels and patterns of green-tree retention on multiple components of the forest ecosystem. Six blocks of forested land in Oregon and Washington were selected as study sites. Four of the DEMO blocks were selected for this mycophagy study, Block 1 (Watson Falls), Block 4 (Dog Prairie), Block 5 (Butte), and Block 7 (Paradise Hills). Block names were derived from local geographic features.

STUDY SITES

The Watson Falls and Dog Prairie blocks are located in the Umpqua National Forest in Oregon; the Paradise Hills and Butte blocks are located in the Gifford Pinchot National Forest in Washington. The blocks were chosen for their accessibility and harvesting ease and access, as well as for forest composition and environmental factors. The dominant tree species in each block is Douglas-fir. The composition of the remaining canopy cover differs among blocks. Although large streams and wetland areas were avoided, the blocks include various environmental gradients. More detailed information concerning the study sites is presented in Halpern *et al.* (1999). The Watson Falls block had been salvaged logged in 1970-1978, and the Dog Prairie block had been thinned in 1986. This management activity occurred one to two decades prior to the initiation of the

DEMO study. Neither the Butte block nor the Paradise Hills block had been managed. Further information on the conceptual framework and establishment of the DEMO study may be found in Aubry *et al.* (1999).

EXPERIMENTAL DESIGN

Within each block, six experimental stands of 13 hectares each were established as treatment units. The treatments were randomly assigned to one unit in each block. Each treatment consisted of a specific green-tree retention level and pattern combination ranging from 15 to 75% retention of the original basal area in a dispersed or aggregated pattern, resulting in a total of five manipulated stands and a control in each block. The treatments were: (1) 100% retention of trees (the control), (2) 75% aggregated retention of the original stand basal area, (3) 40% dispersed retention of the original stand basal area, (4) 40% aggregated retention of original stand basal area, (5) 15% dispersed retention of the original stand basal area, (6) 15% aggregated retention of the original stand basal area (Figure 1, see Aubry *et al.*, 1999 for details). Mycophagy was assessed across four replicates of each treatment – each block provided a complete replicate.
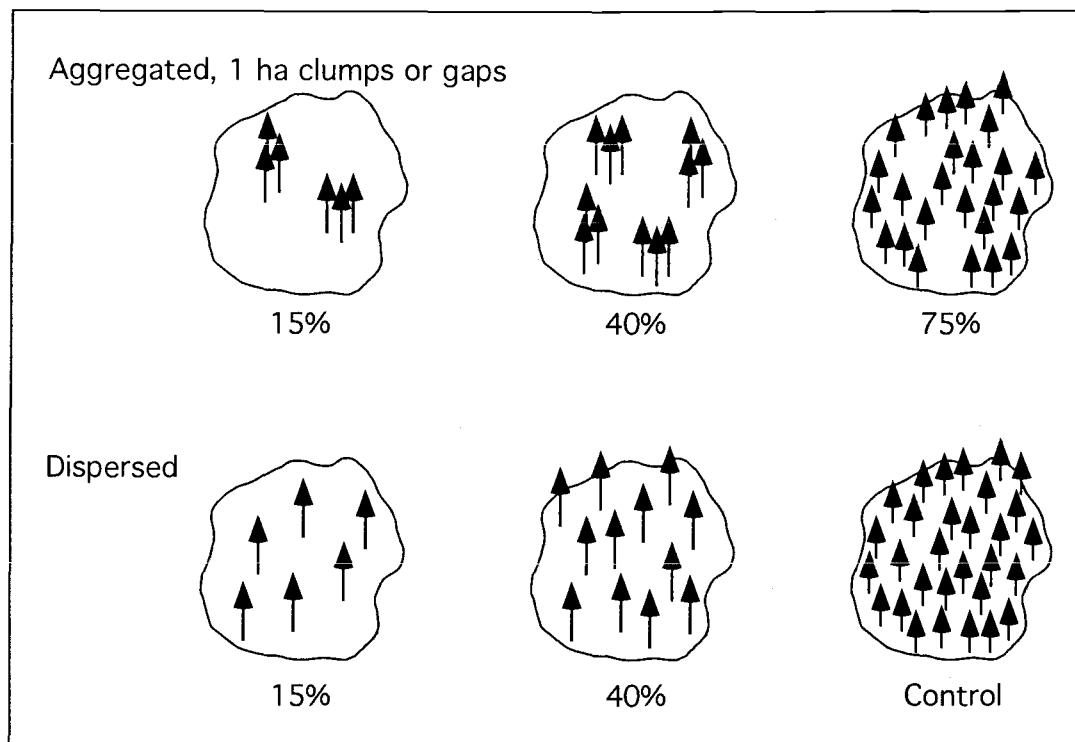
FIGURE 1. DEMO levels and patterns of green-tree retention in percent basal area. Size of units is 13 hectares each.

SMALL MAMMAL SAMPLING

Within each treatment unit, a permanent 8 x 8 or 7 x 9 sampling grid was established. Grid points were spaced 40 meters apart with 40 meters between the grid and the edge of the treatment unit. A Tomahawk 201 live-trap for capturing arboreal rodents (chipmunks and squirrels) and a pitfall trap for small terrestrial mammals (voles) were placed at each grid point. The live traps were baited with a peanut butter and oats mixture and fitted with protection from the elements. The pitfall traps were partially filled with water. Live-traps were set twice each fall for two consecutive four-day periods with two-weeks between the periods, resulting in 16 trap nights per grid point. Trapping was done in each of two years prior to the application of treatments and in each of two years after the application of treatments. Live-traps were checked daily. Pitfall traps were opened for a period of 28 days in the fall and checked weekly. Captured animals constitute the sampling units in this research (See Lehmkuhl *et al.*, 1999, for details).

No *Glaucomys sabrinus* were captured post-treatment in the 15% dispersed retention treatment in the Butte block. Therefore, the 15% dispersed retention treatment was removed from the analysis due to a lack of replication for this animal.

DIET ANALYSIS

For the purposes of the DEMO mycophagy analysis, we are considering *C. gapperi* to be the ecological equivalent of *C. californicus* in the western Cascade

Mountains of Oregon and Washington. Both species are expected to consume relatively equivalent numbers of fungal genera since their habitats in the DEMO study areas are similar. Likewise, the biology, ecology, and habitat of *Tamias siskiyou* and *T. townsendii* are similar in this study, and they are similarly mycophagous. Therefore, they will also be considered ecological equivalents for the purposes of this study.

Fecal pellet analysis is used as a non-lethal method of examining the diets of mycophagous animals (Fogel and Trappe, 1978; Maser *et al.*, 1978; Hayes *et al.*, 1986; Waters and Zabel, 1995; Carey *et al.*, 1999). This methodology allows examination of an animal's recent meals. Methods derived from McIntire and Carey (1989) were used for the analysis of fungal diets.

In each treatment unit, fecal pellets were collected from a maximum of twenty-five animals of each genus each year. One to ten fresh fecal pellets were collected as expelled from each live-trapped animal. Care was taken to avoid the introduction of spores from other materials onto the sample. The fecal material from each individual was placed in a vial of 70% ethanol, marked with identifying numbers and sent to the laboratory. Pellets were collected from pitfall-trapped animals in the lab. In the laboratory, the vials were drained of ethanol and approximately 1.0 ml of de-ionized water per pellet was added. The pellets were macerated with a glass rod and approximately three to five droplets of this solution were placed on a glass slide. To aid in spore identification, a drop of Melzer's reagent (iodine, potassium iodide, and chloral hydrate in aqueous solution) was

added and mixed with the samples on the slide. The liquid sample was evenly distributed on the glass slide and three cover slips per slide were placed side-by-side on top of the fecal sample. The sample was then examined under a compound microscope.

For each of the three cover slips, twenty-five systematically selected, non-overlapping, fields of view were examined at 400x magnification (five rows of five fields each), resulting in a total of 75 fields per fecal sample being examined (Williams, 1987). For each field of view, the presence of each truffle genus was recorded; spores were identified to the genus level using spore morphology and reaction to Melzer's reagent according to Castellano *et al.* (1989). *Truncocolumella, Alpova*, and *Trappea* spores were grouped with *Rhizopogon* spores due to their morphological similarity and the difficulty involved in distinguishing among them. Additionally, the presence of plant material and spores of epigeous sporocarps were recorded for each field of view. For each sample, the frequency of each item was calculated as a percentage of its occurrence in the 75 possible fields. The total number of truffle genera identified in a fecal sample was also recorded. For each animal genus, the pre- and post-treatment total cumulative number of genera was calculated from all samples collected in a treatment unit.

STATISTICAL ANALYSIS

ASSUMPTIONS

Although some types of dietary analyses have been performed using multivariate analysis of variance (Van Horne *et al.*, 1988; Colgan *et al.*, 1997), here the response variables were treated as independent of one another. The response variable for each truffle genus or plant material was calculated as a percent frequency out of a total of 75 fields. The responses were not calculated in relation to one another, nor can the total or relative volumes of dietary items be determined via fecal pellet analysis. Spores in fecal pellets may represent several meals at once, pooled by passage through the gut. Research has shown that while most spores pass through the gut in a matter of hours, many remain in the digestive tract from several days to a month after ingestion (Maser *et al.*, 1986; Pyare and Longland, 2001b). It is unknown whether an animal will eat sporocarps of several truffle genera in a meal or will satiate itself with one sporocarp per meal. Physically, one truffle could be large enough to satisfy the meal requirements of a small mammal. An assumption was made that a small mammal will maximize its use of a truffle before expending energy to search for another. Therefore, each genus was treated as an independent meal in time, and the response of each truffle genus to each treatment was analyzed independently using an analysis of variance (ANOVA).

The number, frequency, distribution, and genera richness of truffles were expected to change in response to the treatments. The potential for parallel changes in the diets of small mammals that feed on truffles was also anticipated. Dietary changes that might be expected include a biologically significant shift in generic composition and dominance in diet items and a shift in the total cumulative number of truffle genera eaten.

AMONG ANIMAL COMPARISONS

To describe and compare the diets among the animal genera studied, only pre-treatment data were used. Mean frequencies of each diet-item for each animal were compared using a one-way ANOVA. The data did not require transformation.

TESTS FOR TREATMENT EFFECTS

For each animal genus examined, six response variables were tested for treatment effects: change in the mean spore frequencies of the four most common genera of truffles in the diets of captured animals (*Gautieria*, *Hysterangium*, *Leucogaster,* and *Rhizopogon*), change in the mean frequency of plant material in the diet, and change in the total cumulative number of truffle genera in the diet. For each of the sample years, mean frequencies for each diet item and the total cumulative number of genera for each animal genus were calculated from the fecal samples of all animals sampled in each treatment unit. The mean frequencies for

the diet items from the two pre-treatment years were averaged to make one pre-treatment mean frequency per diet item.

To determine the change in the frequency of the diet items for each animal genus in each treatment, the mean pre-treatment frequency for each diet item in each treatment was then subtracted from each post-treatment mean frequency for the same treatment to obtain a change in the frequency of each diet item (ex: post-treatment year 1 – pre-treatment mean; post-treatment year 2 – pre-treatment mean). When necessary, truffle spore frequency values were transformed using a hyperbolic arcsine transformation to better meet the assumptions of normal distribution and constant variance.

To determine the change in the total cumulative number of genera in the diet, each treatment pre-treatment total cumulative number of genera was subtracted from the post-treatment total cumulative number of genera.

Due to the complexity inherent in ecological systems, an alpha level of 0.10 was chosen to be appropriate to distinguish statistically significant differences, prior to beginning the data analysis. That alpha level allows detection of treatment effects while protecting against failure to detect a real treatment effect (prevents a Type II error).

A one-way ANOVA was performed on the mean differences for each response variable using STATVIEW (SAS Institute) to detect treatment effects. Main effects for these ANOVA's were block and treatment. Fisher's protected least significant difference (PLSD) was used to determine significant differences in

the change in each response variable in each treatment relative to the control. When the change in a response variable differed significantly from the change in that response variable in the control in more than one treatment, these treatment spore frequencies and/or total cumulative number of genera were then compared to each other for significant differences.

To determine the adequacy of sampling for the total cumulative number of genera in the diet analysis, randomized genus accumulation curves were constructed for each block and treatment combination for each animal genus. The curves were generated by EstimateS version 5.0.1 (Colwell, 1997). Fifty randomized runs of the data were used to construct each curve. Curves for block by treatment combinations that had not approached the asymptote were considered to have an unacceptable number of trapped animals to capture the majority of the genera available to be eaten by the population. These are noted in the results.

The number of replicate blocks differed by animal genus. *Clethrionomys* were trapped in four blocks, whereas *Glaucomys* and *Tamias* were trapped only in two blocks, Watson Falls and Butte. The numbers of fecal samples from each animal genus over the four year period of the study were: *Clethrionomys* 1,185, *Glaucomys* 442, and *Tamias* 569.

RESULTS

DIET COMPARISON AMONG THE SMALL MAMMALS

For all three animal genera, *Rhizopogon* was the most commonly occurring genus in the pre-treatment fecal samples. *Rhizopogon* spores were found in a mean 99.3% of the fields examined in the *G. sabrinus* samples. A mean 97.7% of the fields in the *Clethrionomys* samples had *Rhizopogon* spores, and a mean 98.3% of the fields in the *Tamias* fecal samples contained *Rhizopogon* spores. In the *G. sabrinus* samples, *Gautieria* spores occurred in a mean 54.6% of the fields examined, and were significantly more frequent in the diet of *G. sabrinus* than in the other two animal genera ($p = 0.0480$, Table 1 and Figure 2). Plant material was significantly more common in the diet of the *Tamias* species than in the diet of *G. sabrinus* or the *Clethrionomys* species ($p = 0.0262$ and 0.0397). Plant material was the second most common diet component in the *Clethrionomys* spp., whereas it ranked fourth in the diet of *G. sabrinus*, with a mean frequency of 28.1% (Table 1 and Figure 2). *Hysterangium* spores were significantly less common in the diet of the *Tamias* species than in the diet of *G. sabrinus* or the *Clethrionomys* spp. ($p = 0.0142$ and 0.0980). Only *G. sabrinus* had a high frequency of *Leucogaster* spores in the pre-treatment fecal samples, at 29.1% (Table 1 and Figure 2).

TABLE 1: Among-animal comparisons of the mean frequencies (%) (± SE) of the common truffle genera and plant material and of the mean number of truffle genera (± SE) in the fecal pellets of three small mammal genera captured in four western Oregon and Washington DEMO study blocks, fall 1995 and 1996 (pre-harvest).

Animal	Diet item[1]					Mean number of genera
	Gautieria	*Hysterangium*	*Leucogaster*	*Rhizopogon*	Plant material	
Clethrionomys	16.7 (2.8)^a	11.4 (2.9)^a	4.9 (1.1)^a	97.7 (0.9)	36.2 (2.9)^a	2.2 (0.1)^a
Glaucomys	54.6 (4.9)^b	16.6 (2.7)^a	29.1 (4.2)^b	99.3 (0.6)	28.1 (1.7)^b	3.3 (0.1)^b
Tamias	0.9 (0.6)^c	4.2 (1.5)^b	9.2 (3.6)^a	98.3 (0.9)	49.7 (1.8)^c	1.9 (0.2)^a

[1]Values within a column followed by different superscript letters are significantly different between animals by Fischer's protected LSD, *p*
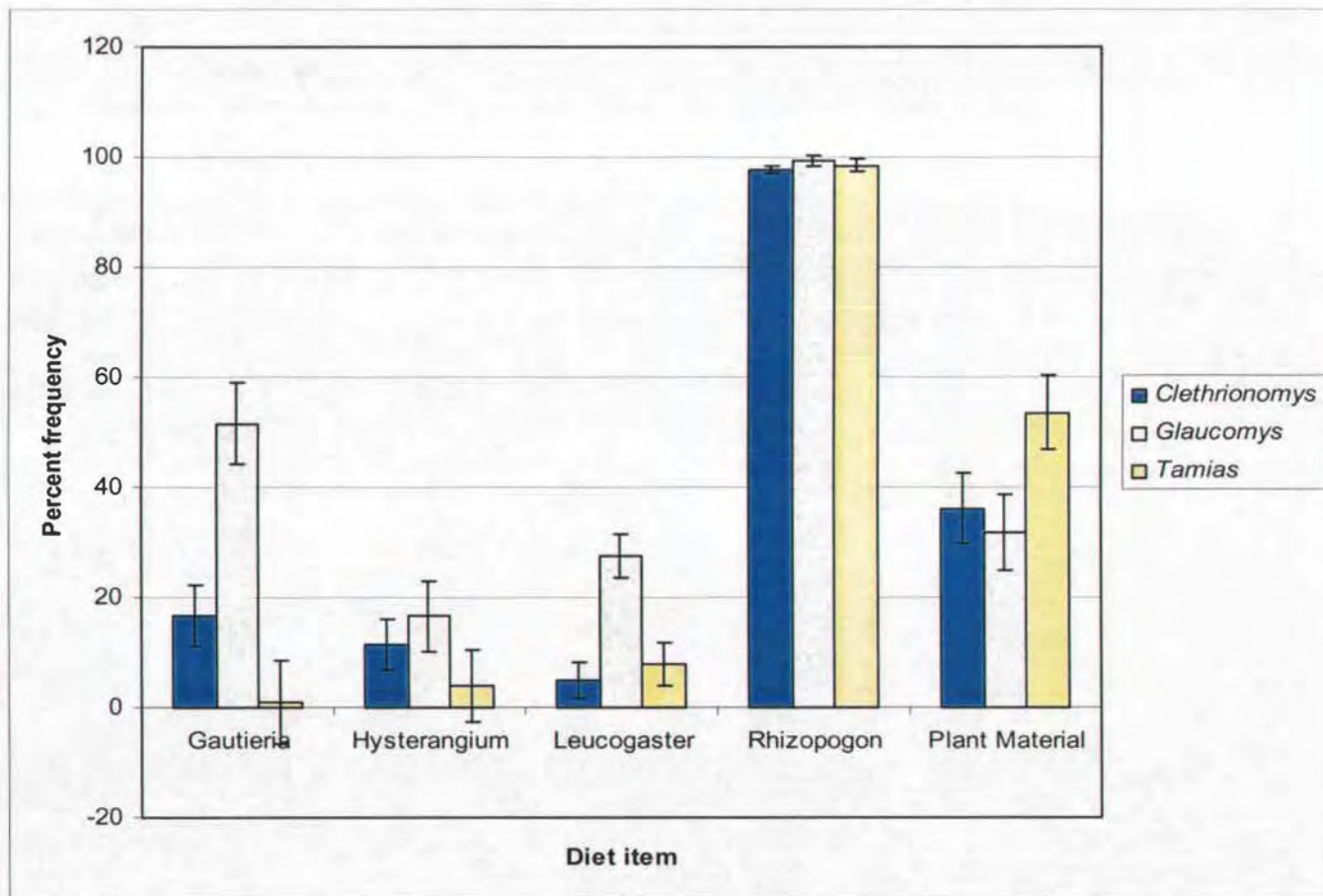
FIGURE 2. Pre-treatment mean frequencies (%) (± SE) of common truffle genera and plant material in the diet of three animal genera sampled from four western Oregon and Washington blocks of the DEMO study, fall 1995 and 1996.

The pre-treatment fecal samples of the *Clethrionomys* species contained spores of a total of 17 different genera of truffles. The *Tamias* and *Glaucomys sabrinus* samples each contained 15 different truffle genera. Differences were observed in the maximum number of genera counted in a single pre-treatment fecal sample: *G. sabrinus* - 10, *Tamias* - 8, and *Clethrionomys* - 5. Pre-treatment *G. sabrinus* fecal samples contained a higher mean number of truffle genera per fecal sample than either the *Tamias* spp. or the *Clethrionomys* spp. samples ($p < 0.0001$ and <0.0001). *G. sabrinus* fecal samples contained the most genera (3.3, Table 1 and Figure 3). The pre-treatment and post-treatment data were pooled for a count of the total number of truffle genera in the diet of each animal genus. A total of 19 truffle genera were identified from the 1,185 *Clethrionomys* samples, 17 genera from the 569 *Tamias* samples, and 16 genera from the 442 *G. sabrinus* samples (Table 2). Fecal samples from each of these animal genera contained minor amounts of spores of the mushroom genus *Laccaria* and spores that could be classified only to the family level: Boletaceae, Cortinariaceae, Entolomataceae, and Russulaceae. Unknown spores presumed to be those of Ascomycota were also occasionally found.
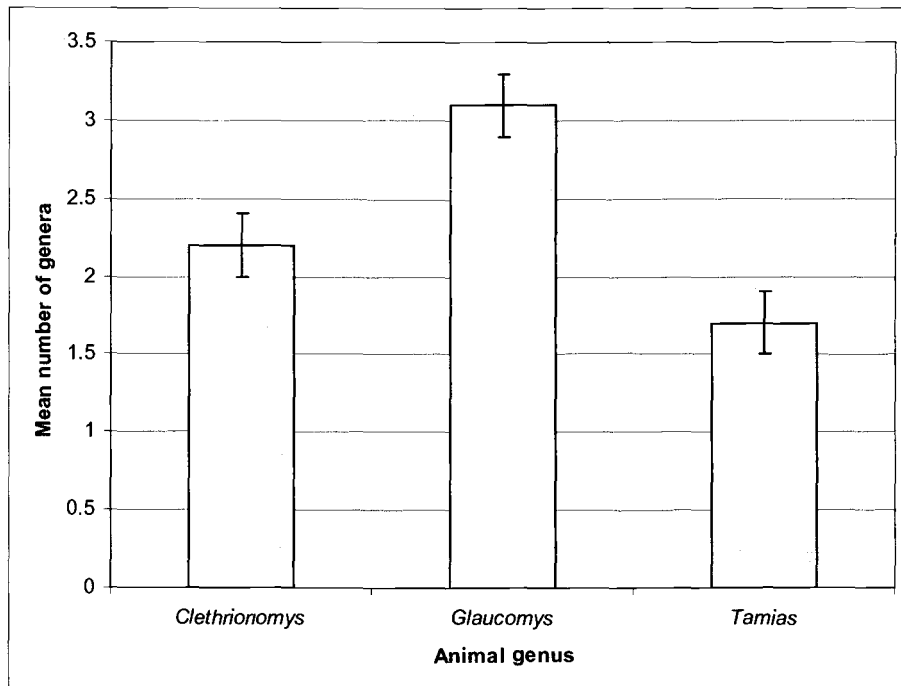
FIGURE 3. Mean number of truffle genera in the pre-treatment diet of three animal genera sampled from four western Oregon and Washington DEMO study blocks, fall 1995 and 1996.

TABLE 2: Constancy[1] of truffle genera found in the fecal pellets of voles, flying squirrels, and chipmunks from four western Oregon and Washington DEMO blocks, combined pre- and post-treatment data, fall 1995 through fall 2000.

Fungal genus	*Clethrionomys* n = 1,185	*Glaucomys* n = 442	*Tamias* 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

[1]Percent of fecal samples with the truffle genus present

CHANGE IN THE DIET OF *CLETHRIONOMYS*

A treatment effect was detected only for the genus *Rhizopogon* ($p = 0.0062$, Table 3). A post-treatment decrease in the frequency of *Rhizopogon* spores in the *Clethrionomys* fecal pellets occurred in all of the treatments (Figure 4), but only the decreases in *Rhizopogon* spore frequency observed in the 75% aggregated ($p = 0.0810$), 40% dispersed ($p = 0.0863$), 40% aggregated ($p = 0.0197$), and 15% aggregated ($p = 0.0005$) retention treatments were significantly different from the change in *Rhizopogon* spore frequency observed in fecal samples from the control. The decrease in *Rhizopogon* spore frequency that was observed in fecal samples from the 15% aggregated retention treatment differed significantly from that observed in the 15% dispersed ($p = 0.0015$), 40% dispersed ($p = 0.0458$) and 75% aggregated ($p = 0.0490$) retention treatments; the decrease in *Rhizopogon* spore frequency in the 15% aggregated and 40% aggregated retention treatments did not differ significantly ($p = 0.1719$) (Table 3).

A treatment effect was also detected for the change in the total cumulative number of genera ($p = 0.0289$, Table 3). The total cumulative number of genera in the *Clethrionomys* fecal pellets increased post-treatment in the control and all treatments except the 40% dispersed retention treatment. In fecal samples from the 40% dispersed retention treatment, the total cumulative number of genera decreased by a mean 1.0 genera (Table 3). The change in the number of genera in the 40% dispersed retention treatment was significantly different from the change in the number of genera observed in the control ($p = 0.0278$). The randomized

genera accumulation curves for the *Clethrionomys* species did not approach the asymptote in the 15% dispersed retention treatment, post-treatment, in the Watson Falls block nor the 15% aggregated retention treatment, post-treatment, in the Dog Prairie block due to the low number of animals captured.
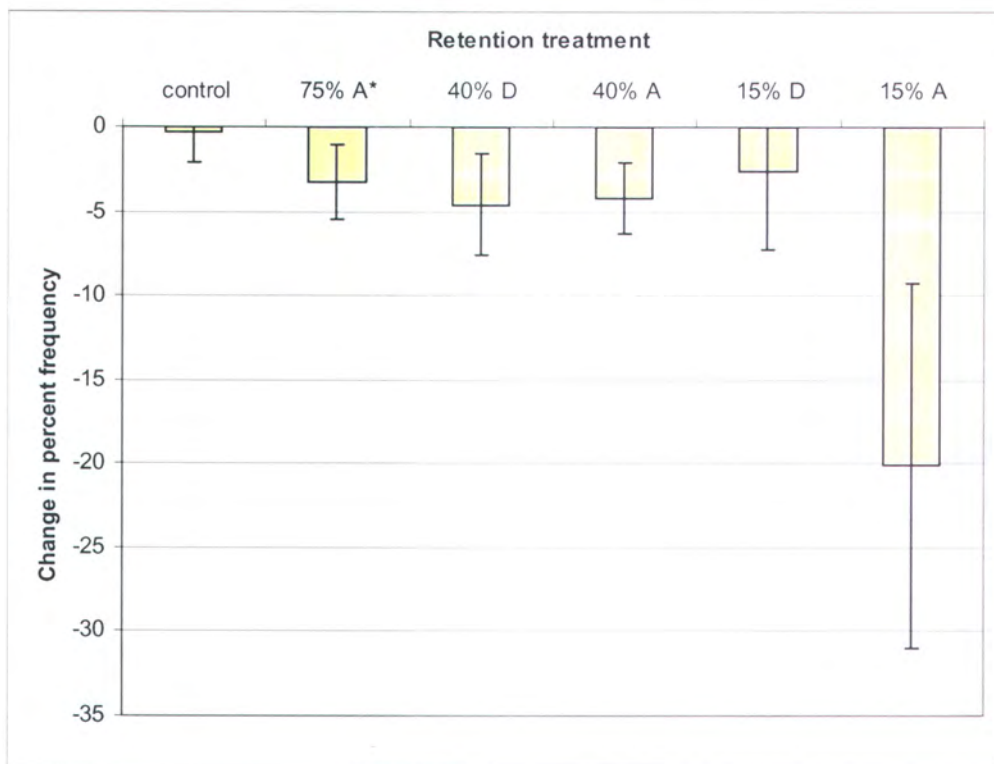
FIGURE 4. Mean change in percent frequency of *Rhizopogon* spores by retention treatment in the diet of *Clethrionomys* captured in four DEMO study blocks, fall 1995 – 2000. *A = aggregated, D = dispersed

TABLE 3. Change in mean frequency (%) (± SE) of diet items and in the mean total cumulative number of genera (± SE) in fecal samples of *Clethrionomys* spp. by diet item and retention treatment with ANOVA results (based on transformed data, when necessary) from four blocks of the DEMO study, fall 1995 – 2000.

Diet item	Retention treatment						Overall ANOVA p-value
	100%	75% A[1]	40% D	40% A	15% D	15% A	
Gautieria	-0.2 (7.5)	-0.1 (4.6)	-6.6 (4.6)	-2.5 (4.7)	0.4 (5.2)	0.8 (5.9)	0.9187
Hysterangium	1.6 (2.6)	1.2 (4.5)	-3.3 (5.0)	-0.8 (1.0)	-5.6 (2.8)	-0.1 (8.0)	0.8550
Leucogaster	4.0 (5.2)	-0.2 (1.0)	-2.7 (2.3)	-1.0 (2.8)	6.2 (4.8)	-0.5 (2.7)	0.5970
Rhizopogon[2]	-0.3^a (1.8)	-3.3^{bd} (2.2)	-4.6^{bd} (3.0)	-4.2^{bc} (2.1)	-2.6^{ad} (4.7)	-20.1^c(10.9)	0.0062
Plant material	3.4 (5.5)	-2.1 (4.0)	5.5 (3.9)	-0.2 (5.6)	4.3 (4.0)	5.2 (3.7)	0.4216
Cumulative number of genera[2]	2.8^{ac} (0.9)	2.0^a (1.1)	-1.0^b (0.7)	4.8^c (1.3)	0.3^a (0.9)	1.0^a (1.7)	0.0289

[1]A = aggregated retention, D = dispersed retention
[2]Diet item change values that are followed by different superscript letters are significantly different between treatments by Fisher's PLSD (p) based on transformed values, when necessary

TABLE 4. Mean frequency (%)(± SE) of diet items and cumulative number of genera (± SE) in fecal samples of *Clethrionomys* spp. pre- and post-treatment by diet item and retention treatment in four blocks of the DEMO study, fall 1995 – 2000.

Diet item	Condition	Retention treatment					
		100%	75% A[1]	40% D	40% A	15% D	15% A
Gautieria	Pre[2]	19.8 (8.5)	17.8 (5.8)	15.5 (7.2)	16.6 (7.8)	8.6 (6.6)	18.7 (6.9)
	Post[2]	20.0 (8.2)	17.7 (6.2)	8.9 (2.3)	14.2 (3.2)	9.0 (7.2)	19.6 (7.1)
Hysterangium	Pre	4.8 (1.7)	15.2 (8.1)	8.9 (4.6)	3.5 (1.3)	9.8 (5.7)	23.6 (12.6)
	Post	6.4 (3.2)	16.5 (7.3)	5.6 (3.4)	2.7 (1.0)	4.2 (2.8)	23.6 (12.6)
Leucogaster	Pre	6.3 (2.6)	3.5 (1.9)	4.6 (2.3)	5.6 (3.7)	3.1 (2.2)	6.3 (3.1)
	Post	10.9 (4.1)	3.4 (1.0)	1.9 (1.5)	4.6 (1.6)	9.3 (5.3)	5.8 (3.2)
Rhizopogon	Pre	97.1 (1.5)	99.7 (0.3)	95.7 (4.3)	98.3 (1.0)	96.9 (2.0)	99.9 (0.1)
	Post	96.8 (2.3)	96.4 (2.1)	91.1 (5.8)	94.1 (2.1)	94.3 (4.2)	79.8 (10.9)
Plant material	Pre	38.7 (9.8)	41.9 (8.8)	30.3 (7.0)	41.7 (8.6)	32.8 (5.5)	31.4 (3.4)
	Post	42.1 (5.8)	39.7 (4.7)	38.4 (5.1)	41.5 (5.0)	37.1 (4.5)	36.5 (4.4)
Cumulative number of genera	Pre	5.5 (1.0)	6.8 (0.8)	6.5 (0.9)	5.8 (0.8)	6.0 (0.7)	6.8 (1.3)
	Post	8.3 (1.0)	8.8 (1.7)	5.5 (0.5)	10.5 (1.0)	6.3 (1.3)	7.8 (1.4)

[1] A = aggregated retention, D = dispersed retention
[2] Pre = pre-treatment condition, post = post-treatment condition

CHANGE IN THE DIET OF *GLAUCOMYS SABRINUS*

Results for the 15% dispersed retention treatment are not included because no animals were trapped post-treatment in the Butte replicate. A treatment effect was detected only for the mean change in frequency of *Gautieria* spores in the diet of *G. sabrinus* ($p = 0.0442$, Table 5 and Figure 5). In the 40% dispersed retention, *Gautieria* spores increased by a frequency of 32.6% above that seen in fecal samples from the control ($p = 0.0607$, Table 5 and Figure 5). Percent frequency of *Gautieria* spores in fecal samples from animals in the 40% aggregated retention treatment exhibited a mean decrease of 22.8% post-treatment ($p = 0.0994$, Table 5 and Figure 5). The changes in frequency of *Gautieria* spores in samples from the 40% aggregated and 40% dispersed retention treatments were significantly different from one another ($p = 0.0045$).

There was no change in the mean total cumulative number of truffle genera in the diet of *G. sabrinus* ($p = 0.1906$). Genera accumulation curves indicated that a minimum of 8 animals was generally sufficient to observe most of the genera available to be eaten by both *G. sabrinus* and the *Tamias* spp. The post-treatment randomized genera accumulation curves for *Glaucomys sabrinus* did not approach the asymptote in the 40% aggregated, 40% dispersed, and 15% aggregated retention treatments in the Watson Falls block nor the 40% dispersed retention treatment in the Butte block due to the low number of animals captured.

FIGURE 5. Mean change in percent frequency of *Gautieria* spores by retention treatment in the diet of *Glaucomys sabrinus* captured in two DEMO study blocks, fall 1995 – 2000. *A = aggregated, D = dispersed

TABLE 5. Change in mean frequency (%) (± SE) of diet items and in the mean total cumulative number of genera (± SE) in fecal samples of *Glaucomys sabrinus* by diet item and retention treatment with ANOVA results (based on transformed data, when necessary) from two blocks of the DEMO study, fall 1995 – 2000.

Diet item	Retention treatment					Overall ANOVA *p*-value
	100%	75% A[1]	40% D	40% A	15% A	
Gautieria[2]	0.2[a] (9.6)	6.8[ab](12.5)	32.8[b] (4.4)	-22.8[c] (7.0)	-7.0[ac] (3.9)	0.0442
Hysterangium	21.0 (11.7)	8.7 (6.4)	-0.5 (0.2)	16.9 (9.6)	43.8 (12.2)	0.1524
Leucogaster	13.1 (3.7)	32.5 (4.5)	42.4 (36.7)	5.0 (7.2)	23.9 (12.0)	0.2320
Rhizopogon	0.3 (0.1)	0 (0)	0 (0)	1.9 (3.8)	0.01 (0.003)	0.9419
Plant material	17.6 (9.1)	4.5 (9.1)	17.0 (0.5)	11.1 (3.9)	21.5 (9.4)	0.5128
Cumulative number of genera[3]	2.5 (0.5)	2.5 (2.5)	-3.5* (0.5)	3.5 (3.5)	-2.0 (3.0)	0.1906

[1]A = aggregated retention, D = dispersed retention
[2]Diet item change values that are followed by different superscript letters are significantly different between treatments by Fisher's PLSD (*p*
[3]*significantly different from control at *p*   .

TABLE 6. Mean frequency (%)(± SE) of diet items and cumulative number of genera (± SE) in fecal samples of *Glaucomys sabrinus* pre- and post-treatment by diet item and retention treatment in two blocks of the DEMO study, fall 1995 – 2000.

Diet item	Condition	Retention treatment									
		100%		75% A[1]		40% D		40% A		15% D	
Gautieria	Pre[2]	61.1	(0.5)	53.0	(6.6)	40.9	(22.7)	52.3	(8.9)	73.4	(12.3)
	Post[2]	61.2	(9.7)	59.8	(11.8)	73.7	(18.4)	29.6	(11.3)	65.7	(10.3)
Hysterangium	Pre	10.3	(5.0)	19.4	(8.0)	11.4	(10.9)	17.8	(12.2)	16.0	(1.1)
	Post	31.2	(11.3)	28.1	(9.2)	11.0	(11.0)	34.7	(14.0)	59.4	(13.0)
Leucogaster	Pre	33.2	(24.1)	34.1	(1.4)	12.3	(6.0)	33.0	(2.7)	35.7	(13.8)
	Post	46.2	(10.9)	66.6	(4.2)	54.7	(42.7)	37.9	(7.5)	55.0	(7.5)
Rhizopogon	Pre	99.8	(0.3)	100	(0)	100	(0)	96.2	(3.9)	99.9	(0.05)
	Post	100	(0)	100	(0)	100	(0)	98.0	(2.0)	100	(0)
Plant material	Pre	21.3	(4.3)	29.1	(4.6)	30.0	(2.2)	32.6	(3.8)	23.2	(1.5)
	Post	38.9	(10.5)	33.6	(7.4)	46.7	(2.7)	43.7	(4.6)	44.2	(9.7)
Cumulative number of genera	Pre	7.0	(1.0)	9.0	(2.0)	8.0	(0)	7.0	(2.0)	8.5	(0.5)
	Post	9.5	(0.5)	11.5	(0.5)	4.5	(0.5)	10.5	(1.5)	6.5	(2.5)

[1] A = aggregated retention, D = dispersed retention
[2] Pre = pre-treatment condition, post = post-treatment condition

CHANGE IN THE DIET OF *TAMIAS*

The mean change in frequency of *Rhizopogon* spores in the fecal samples of the *Tamias* spp. exhibited a treatment effect ($p = 0.0613$, Table 7). The frequency of *Rhizopogon* spores in samples from the 15% dispersed retention treatment showed a change in frequency significantly different from that seen in samples from the control ($p = 0.0844$); *Rhizopogon* spore frequency decreased by a mean 2.5% in samples from the 15% dispersed retention treatment while frequency of *Rhizopogon* spores in the control samples increased by a mean of 1.7% (Figure 6).

There was no treatment effect for the change in the total cumulative number of truffle genera in the diet of the *Tamias* spp. ($p = 0.1906$). The pre-treatment randomized genera accumulation curves for the *Tamias* spp. did not approach the asymptote for any of the treatments in the Watson Falls block, except the 40% dispersed retention.
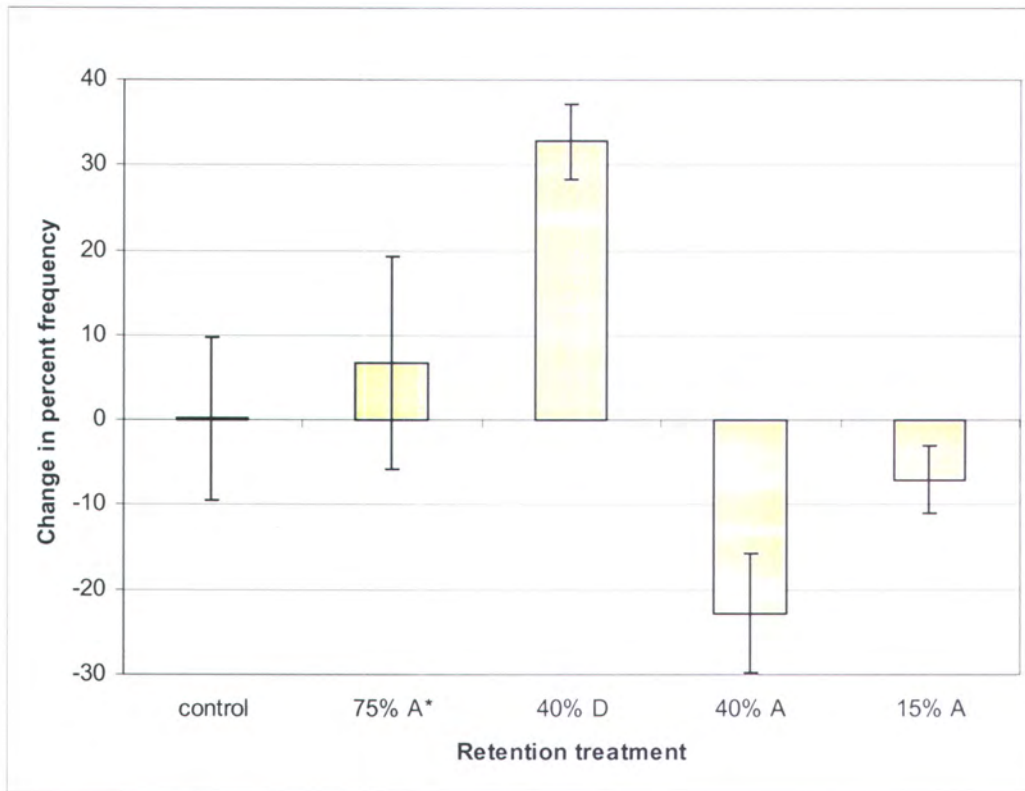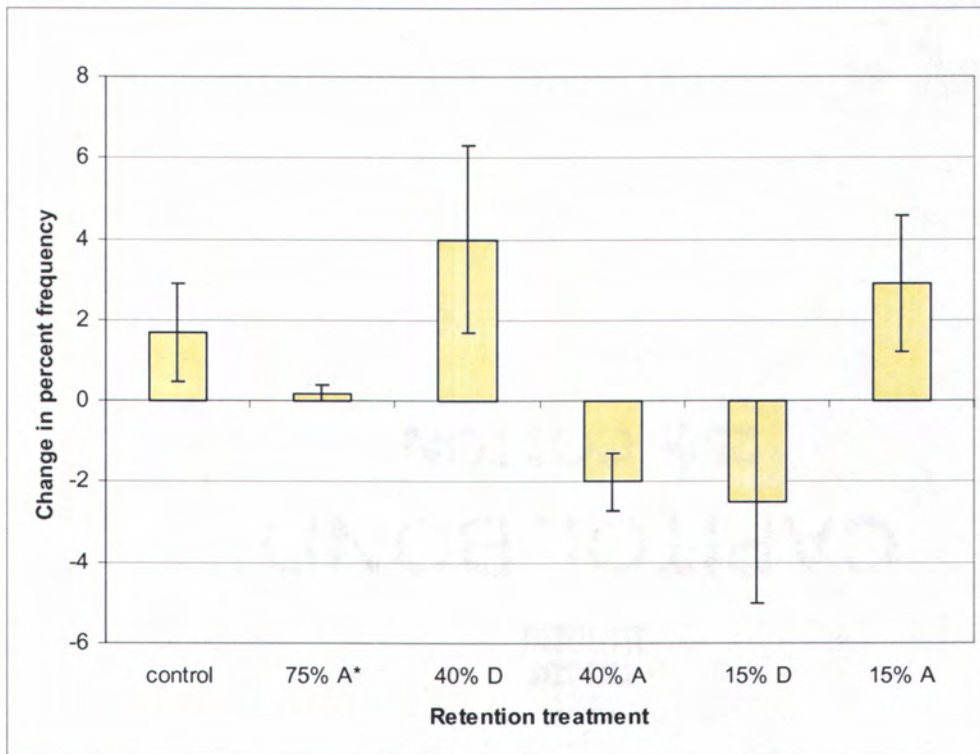
FIGURE 6. Mean change in percent frequency of *Rhizopogon* spores by retention treatment in the diet of *Tamias* captured in two DEMO study blocks, fall 1995 – 2000. *A = aggregated, D = dispersed

TABLE 7. Change in mean frequency (%) (± SE) of diet items and in the mean total cumulative number of genera (± SE) in fecal samples of *Tamias* by diet item and retention treatment with ANOVA results (based on transformed data, when necessary) from two blocks of the DEMO study, fall 1995 – 2000

Diet item[2]	Retention treatment						Overall ANOVA p-value
	100%	75% A[1]	40% D	40% A	15% D	15% A	
Gautieria	7.3 (1.1)	1.5 (1.1)	0.8 (2.1)	2.9 (4.2)	0.5 (2.0)	9.6 (6.1)	0.4856
Hysterangium	13.6 (8.9)	-0.1 (1.5)	10.7 (6.9)	9.7 (11.4)	3.2 (4.5)	8.5 (5.3)	0.7531
Leucogaster	9.3 (9.1)	1.9 (6.5)	11.5 (6.8)	-4.5 (4.8)	10.6 (11.3)	9.6 (8.2)	0.7098
Rhizopogon	1.7^{ab} (1.2)	0.2^{abc} (0.2)	4.0^{a} (2.3)	-2.0^{bc} (0.7)	-2.5^{c} (2.5)	2.9^{a} (1.7)	0.0613
Plant material	-10.7 (8.1)	-10.2 (8.6)	-16.4 (8.9)	-6.0 (9.4)	-11.2 (4.1)	-7.7 (4.4)	0.9510
Cumulative number of genera	4.5 (1.5)	5.0 (0)	5.0 (0)	6.0 (2.0)	6.0 (2.0)	4.5 (1.5)	0.6664

[1]A = aggregated retention, D = dispersed retention
[2]Diet item change values that are followed by different superscript letters are significantly different between treatments by Fisher's PLSD (p 0.10) based on transformed values, when necessary.

TABLE 8. Mean frequency (%)($\pm$ SE) of diet items and cumulative number of genera ($\pm$ SE) in fecal samples of the *Tamias* spp. pre- and post-treatment by diet item and retention treatment in two blocks of the DEMO study, fall 1995 – 2000

Diet item	Condition	Retention treatment					
		100%	75% A[1]	40% D	40% A	15% D	15% A
Gautieria	Pre[2]	0.3 (0.3)	0.3 (0.3)	2.5 (1.9)	4.5 (4.5)	2.6 (2.4)	2.6 (2.4)
	Post[2]	7.6 (1.1)	1.8 (1.1)	3.3 (1.7)	7.4 (3.5)	3.1 (1.8)	12.2 (5.1)
Hysterangium	Pre	2.0 (1.1)	2.6 (2.4)	7.8 (6.7)	9.1 (1.9)	3.0 (3.0)	6.9 (0.3)
	Post	15.6 (9.0)	2.6 (1.6)	18.4 (7.3)	18.7 (11.8)	6.1 (3.6)	15.4 (5.4)
Leucogaster	Pre	12.0 (5.2)	15.5 (11.7)	6.6 (1.5)	18.4 (15.5)	6.8 (5.3)	5.8 (5.6)
	Post	21.2 (6.8)	17.3 (3.9)	18.1 (6.3)	14.0 (5.4)	17.4 (13.0)	15.4 (7.1)
Rhizopogon	Pre	98.1 (2.0)	99.7 (0.3)	95.5 (4.5)	100 (0)	100 (0)	96.8 (3.2)
	Post	99.8 (0.2)	99.8 (0.1)	99.5 (0.4)	98.1 (0.7)	97.5 (2.5)	99.6 (0.3)
Plant material	Pre	49.8 (6.2)	48.2 (4.5)	58.9 (12.6)	49.3 (13.6)	54.2 (0.6)	58.1 (1.9)
	Post	39.1 (9.1)	38.0 (7.0)	42.5 (10.1)	43.3 (4.7)	43.0 (4.1)	50.4 (3.4)
No. of Genera	Pre	4.5 (1.5)	5.5 (0.5)	5.0 (1.0)	5.0 (0)	4.0 (1.0)	3.5 (2.5)
	Post	9.0 (0)	10.5 (0.5)	10.0 (1.0)	11.0 (2.0)	10.0 (0)	8.0 (1.0)

[1] A = aggregated retention, D = dispersed retention
[2] Pre = pre-treatment condition, post = post-treatment condition

DISCUSSION

PRE-TREATMENT DIETS

Due to low capture numbers during the pre-treatment years, frequencies of fungal genera in the feces of the *Tamias* spp. were calculated from only 42 animals, whereas the values for *Glaucomys sabrinus* were calculated from 175 animals and the *Clethrionomys* spp. frequencies from 458 animals.

As expected, due to their different feeding habits, the pre-treatment diets of the *Tamias* spp., the *Clethrionomys* spp., and *Glaucomys sabrinus* differed. *Clethrionomys* are known to be highly mycophagous, eating a diverse array of truffle genera (Ure and Maser, 1982; Hayes *et al.*, 1986; Maser *et al.*, 1986; Maser and Maser, 1988). Although multiple truffle genera were represented in the feces of the *Clethrionomys* in this study, spores of the most common truffle genera were more frequent in the *G. sabrinus* samples.

A study examining diet differences between *C. gapperi* and *C. californicus* by Maser and Maser (1988) showed a moderate frequency of multiple truffle genera represented in the feces, with *Rhizopogon* spores being the most common. A moderate frequency of multiple truffle genera was found in the diet of the *Clethrionomys* in this study as well. Although *G. sabrinus* fecal samples contained a higher mean number of genera per sample in this study, the *Clethrionomys* spp. had the highest total number of truffle genera in their feces when the pre- and post-

treatment data was pooled. However, nearly twice as many *Clethrionomys* fecal samples were examined than either *Glaucomys* or *Tamias* samples.

G. sabrinus has been described as a fungal specialist, utilizing a diverse array of fungi for the majority of its diet (Maser *et al.*, 1986; Carey *et al.*, 1999; Claridge *et al.*, 1999). Within the DEMO units, fecal samples from *G. sabrinus* showed high mean frequencies for several fungal genera, supporting this description. In this study, *G. sabrinus* had the highest number of genera in a single fecal sample as well as the highest mean number of genera per sample. Cázares *et al.* (1999) found relatively high mean frequencies of the same truffle genera represented in the feces of *G. sabrinus* from earlier pre-treatment sampling of the Watson Falls DEMO block.

Maser *et al.* (1986) described the northern flying squirrel as a truffle generalist, with no preference for specific truffle genera. However, Maser *et al.* (1986) compared the fluctuation in spore frequency in the feces of *G. sabrinus* with "previously established" fruiting patterns of the truffles found in the feces. Maser *et al.* (1986) did not measure truffle biomass in the study area concurrently with truffle spore frequency in the diets of *G. sabrinus*. Without direct comparison of truffle consumption versus available biomass, the conclusion that *G. sabrinus* does not prefer certain truffle genera is unwarranted and contradicted by other lines of evidence.

In this study, the high frequency of *Gautieria* spores in the diet of *G. sabrinus* compared to the low frequency of *Gautieria* in the diets of the

Clethrionomys and *Tamias* spp. indicates that *G. sabrinus* has at least a relative preference for *Gautieria* truffles (Table 1). Food trials on northern flying squirrels performed by Zabel and Waters (1997) indicated that, out of the truffle genera offered to the animals, *Gautieria* sporocarps were most commonly eaten. However, their food trial did not include *Rhizopogon* truffles, the most ubiquitous spore type from fecal samples in several studies. Colgan *et al.* (1997) found *Gautieria* spores to be common in the feces of *G. sabrinus*, but to be absent in the feces of *T. townsendii*, and Cázares *et al.* (1999) found the frequency of *Gautieria* spores to be higher in *G. sabrinus* fecal pellets than in *Tamias siskiyou* or *Clethrionomys californicus* pellets. Carey *et al.* (2002) found that *Gautieria* spores occurred with greater rank frequency in *G. sabrinus* diets than the rank of sporocarp frequency in the squirrels' habitat. Their data show (Table 2, Carey *et al.*, 2002) that *Gautieria* spores are about as frequent in fecal pellets as *Hysterangium* spores even though *Hysterangium* truffles were found with 4 – 17 times greater frequency. Consequently, their results further support the interpretation that *G. sabrinus* selects for *Gautieria* truffles when feeding. *Gautieria* sporocarps emit particularly strong odors which may make them easier to detect than other truffles; however, other small mammals consume *Gautieria* less frequently than *G. sabrinus*. The cumulative evidence suggests that *G. sabrinus* prefers eating *Gautieria*, especially compared to other small mammals.

The *Tamias* spp. appear to be the least reliant upon a varied fungal diet, with a low presence of the common truffle genera except for the nearly

omnipresent *Rhizopogon* spores. Plant material was the second most common diet item for the *Tamias* spp., occurring with 13.5% more frequency than in *Clethrionomys* samples, and with 21.6% more frequency than in *Glaucomys* samples. Colgan *et al.* (1997) also found plant material to be heavily represented in the diet of *T. townsendii*, ranking second in dietary importance. In contrast to the results presented here, fecal samples from *Tamias* in the Colgan *et al.* (1997) study contained a high mean frequency of *Hysterangium* spores and almost no *Leucogaster* spores, whereas *Tamias* in this study had slightly higher frequencies of *Leucogaster* than *Hysterangium* spores. Luoma *et al.* (1991) found that *Leucogaster* sporocarp production was higher than *Hysterangium* on dry sites, particularly in summer. *Hysterangium* biomass exceeded that of *Leucogaster* on mesic sites, particularly in spring. The difference between the *Hysterangium* and *Leucogaster* mean frequencies in the fecal samples from these two studies is probably related to season of trapping and habitat differences that affect relative sporocarp abundance.

A previous mycophagy study performed in the Watson Falls block of the DEMO study showed that *Leucogaster* spores were more frequent in the diet of *T. siskiyou* than *C. californicus* (Cázares *et al.*, 1999). In this study, only *G. sabrinus* had a high frequency of *Leucogaster* spores; the frequency of *Leucogaster* spores in the diets of the *Tamias* spp. and the *Clethrionomys* spp. did not significantly differ. The discrepancy in these results may be due to a block effect, as only one block was examined in Cázares *et al.* (1999). The pre-treatment fecal samples of

the *Tamias* spp. from the Watson Falls block in this study had twice the frequency of *Leucogaster* spores as compared to samples from the Butte block, indicating that *Tamias* captured in Watson Falls ingested greater amounts of *Leucogaster* truffles than *Tamias* in the Butte block. Pre-treatment *Leucogaster* sporocarp biomass averaged six times more in the Watson Falls block compared to the Butte block (D. Luoma, unpublished data).

Although a diversity of truffle genera were represented in moderate frequencies in the *Tamias* fecal samples, it was uncommon for a fecal sample to have a high frequency of spores other than *Rhizopogon*. McIntire (1984) also found *Rhizopogon* to be the most frequently represented truffle genus in the feces of *T. siskiyou*. In this study, a more diverse array of genera was more consistently found in the diets of both *G. sabrinus* and the *Clethrionomys*. Flying squirrel diets tend to be more consistently diverse than *Tamias* or even *Clethrionomys* diets (Carey *et al.*, 1999). Results from these different studies support the description of this chipmunk by Maser *et al.* (1978) as an "avid mycophagist," rather than a fungal specialist.

The high diversity of fungal genera in the diets of these small mammals emphasizes the importance of mycophagy as a spore dispersal mechanism for the ectomycorrhizal fungi that produce truffles. These animals may prefer some truffles over others or are more strongly attracted by odor to certain truffles (Trappe and Maser, 1977; Donaldson and Stoddart, 1994; Pyare and Longland, 2001b).

CHANGE IN THE DIETS

Consideration of the results from the *Glaucomys sabrinus* analysis should take into account the low number of replicates involved in the analysis. Additionally, in a few experimental units, only one animal (sample unit) was captured in a given treatment in a given year, which limits the ability to moderate the variance associated with the change in frequency of a fungal genus. In some cases the treatment eliminated *G. sabrinus* from an experimental unit. In the Watson Falls block, no *G. sabrinus* were captured post-treatment in the 15% dispersed retention treatment, post-treatment year 2 (2000) in the 40% dispersed retention treatment, or post-treatment year 1 (1999) in the 15% aggregated retention treatment. Due to the lack of post-treatment replication, the change in mean genera percent frequency could not be calculated for the 15% dispersed retention treatment and this treatment was removed from the analysis.

When constructing fungal spore genus accumulation curves, it was noted that in four block x treatment x condition combinations, the genus accumulation curves did not approach an asymptote. Because many of the truffle genera that *G. sabrinus* could eat were not accounted for in these combinations, it was not possible to test for treatment effects on mean total cumulative genus richness in those cases.

The *Tamias* data, like the *Glaucomys* data, contains combinations with limited sample units, in some cases as few as two animals were captured in a

specific block x treatment x condition combination. Additionally, *Tamias* data from only one pre-treatment year were available for the Watson Falls block. Discussion of the results is presented with these factors in mind.

Clethrionomys

The frequency of *Rhizopogon* spores decreased significantly in fecal samples from all treatments compared to the decrease in the control except in samples from the 15% dispersed retention treatment (Table 3). The genus *Rhizopogon* was the most common truffle on the sample plots (D. Luoma, unpublished data) and was also the most common spore in the feces of all of the animal genera examined. The spores of this genus are so common in the fecal samples examined in this study that they were typically in 100% of the fields examined.

Because the samples were swamped with *Rhizopogon* spores, an even larger than estimated decrease of *Rhizopogon* truffles in the diet of an animal must occur for the change to be detected by spore frequency measurements (Williams, 1987). A large decrease of *Rhizopogon* truffles in an animal's diet could occur either by physical habitat changes (the removal of trees) that would severely limit access to *Rhizopogon* truffles or by a large decrease in the abundance or frequency of *Rhizopogon* truffles within a treatment unit.

The diet of *Clethrionomys* from the 15% aggregated retention showed the largest decrease in *Rhizopogon* spore frequency (Table 3). *Rhizopogon* truffle

biomass significantly decreased in the 15% aggregated retention treatment (D. Luoma, unpublished data; Table 11) and *Clethrionomys* captures significantly increased (C. Maguire and S. West, unpublished data, see Tables 9 and 10). Both of these measured factors could influence the ability of *Clethrionomys* to forage for *Rhizopogon* truffles, as the increase in the number of animals would increase the competition for truffles, and the decrease in biomass would mean fewer truffles would be available. The combination of the increased competition for sporocarps and the decrease in available *Rhizopogon* sporocarp biomass should decrease the average availability of *Rhizopogon* truffles for consumption as compared to the pre-treatment condition. However, *Clethrionomys* captures increased in all treatments (C. Maguire and S. West, unpublished data; Tables 9 and 10), and *Rhizopogon* biomass also decreased in the 15% dispersed and 40% aggregated retention treatments (D. Luoma, unpublished data; Table 11), yet no similarly large decrease in *Rhizopogon* spore frequency was observed in animals from those treatments. The movement of *Clethrionomys* in the 15% aggregated retention treatment is severely restricted due to their habitat requirements, severely limiting access to alternate sources of *Rhizopogon* truffles.

Recently-harvested clearcuts are generally considered unsuitable habitat for *Clethrionomys* (Gashwiler, 1970). In the DEMO aggregated retention treatments, vole captures were strongly associated with the tree aggregates, suggesting that the aggregates are acting as habitat refuges, and the movement of these animals may be restricted within a treatment unit, creating an "island effect." In the 40%

aggregated retention treatment, the aggregates are closer together than those in the 15% aggregated retention treatment. *Clethrionomys* in the 40% aggregated retention treatment may still be able to travel across the smaller clearcut areas in this treatment to reach other aggregates or the edge of the treatment. In the 15% aggregated retention unit, the majority of the unit is devoid of trees and the aggregates are widely separated. *Clethrionomys* in these aggregates would have to cross a large bare expanse of land in order to reach another aggregate or the edge of the treatment. Research has shown that *Clethrionomys* are rarely found in clearcuts (Gashwiler, 1970). This restriction of movement further intensifies competition for *Rhizopogon* sporocarps, as a larger *Clethrionomys* population must compete for the dwindling biomass of *Rhizopogon* truffles in this treatment.

Mills (1995) recognized a strong negative edge effect for both *Clethrionomys* numbers and sporocarp abundance in 0.6 – 2.5 hectare forest remnants, both decreased with decreasing distance to edge. As the DEMO aggregates are 1.0 hectare in size, a strong negative edge effect is probable; this tight aggregation of trees in a circular pattern would create a large amount of edge area. Thus, not only are the voles restricted from traveling as far as they would in a continuous forest, but their movement may be further concentrated towards the center of the aggregates by the edge effect. *Rhizopogon* truffle abundance heavily declined in the clearcut areas and may decrease towards the edge of the aggregate, something that would not necessarily show up in the overall truffle biomass for a treatment. Limitation of vole movement combined with the reduction in truffle

abundance could reduce the mean availability and diversity of truffles. These results indicate that for the *Clethrionomys* species, overall, the harvesting of trees reduces the frequency of *Rhizopogon* spores in the diet, and that the isolated aggregate pattern (15%) exacerbated this effect.

The combination of the increased competition for sporocarps and the decrease in available *Rhizopogon* sporocarp biomass should decrease average availability of *Rhizopogon* truffles for consumption as compared to the pre-treatment condition. However, these changes did not completely explain the reduction in *Rhizopogon* spore frequency observed in several of the treatments, indicating that other factors are involved as well.

TABLE 9: Mean change in number of captures per 100 trap nights ($\pm$ SE) for each animal genus by green-tree retention treatment with ANOVA results (based on transformed data, when necessary) $n = 2$.

Animal	Retention treatment						Overall ANOVA p-value
	100%	75% A[1]	40% D	40% A	15% D	15% A	
Clethrionomys[2,3]	27.0[a] (7.6)	8.9[b] (12.6)	43.4[ab](28.6)	27.9[ab](13.9)	10.8[b](19.3)	8.4[b](12.6)	<0.0001
Glaucomys	-0.4[a] (0.5)	-0.9[b] (0.3)	-1.5[c] (0.03)	-1.7[c] (0.9)	-1.7[c] (0.1)	-2.1[d] (0.1)	<0.0001
Tamias	-2.8[a] (1.6)	-1.6[b] (0.9)	-4.8[c] (1.9)	-4.0[c] (1.4)	-1.4[b] (0.4)	-1.9[b] (0.5)	<0.0001

[1] A = aggregated, D = dispersed
[2] Capture change values that are followed by different superscript letters are significantly different between treatments by Fisher's PLSD (p
[3] Clethrionomys captures reflect change in total captures rather than captures per trap night

TABLE 10. Mean number of captures per 100 trap nights (± SE) for each animal genus by green-tree retention treatment, pre- and post-treatment.

Animal	Condition[2]	Treatment					
		100%	75% A[1]	40% D	40% A	15% D	15% A
Clethrionomys[2,3]	Pre	21.3 (5.0)	27.8 (6.4)	28.4 (3.6)	27.0 (4.6)	30.1 (8.3)	25.9 (3.9)
	Post	48.3 (10.1)	36.6 (9.7)	71.8 (28.9)	54.9 (13.4)	40.9 (15.1)	34.3 (12.2)
Glaucomys	Pre	1.5 (0.4)	2.1 (0.01)	1.6 (0.1)	2.4 (1.3)	1.8 (0.3)	2.5 (0.4)
	Post	1.1 (0.3)	1.2 (0.3)	0.2 (0.1)	0.7 (0.1)	0.2 (0.1)	0.4 (0.2)
Tamias	Pre	6.7 (3.1)	4.0 (1.1)	6.2 (2.7)	6.6 (2.8)	3.4 (0.3)	3.6 (0.1)
	Post	3.9 (0.5)	2.4 (0.3)	1.3 (0.4)	2.6 (0.2)	2.0 (0.5)	1.7 (0.5)

[1]A = aggregated, D = dispersed
[2]Pre = pre-treatment condition, post = post-treatment condition
[3]*Clethrionomys* captures reflect change in total captures rather than captures per trap night

TABLE 11. Mean fall truffle biomass (g/ha) (± SE) by green-tree retention treatment of those genera showing significant pre- and post-treatment differences, $n = 3$.

Truffle genus	Condition[1]	Retention treatment					
		100%	75% A[2]	40% D	40% A	15% D	15% A
Gautieria	Pre	0	0	60	70	410	20
	Post	110	0	0^3	20^3	0^3	0^3
Rhizopogon	Pre	1240	980	1070	620	1350	770
	Post	930	790	760	75^3	120^3	20^3

[1]Pre = pre-treatment condition, post = post-treatment condition
[2]A = aggregated, D = dispersed
[3]Denotes statistically significant post-treatment changes by genus within a treatment using Fisher's protected LSD, p 05, on transformed data

Glaucomys sabrinus

Since *Gautieria* truffles appear to be a preferred food of *G. sabrinus*, the significant change in *Gautieria* spore frequency in the 40% aggregated and 40% dispersed retention treatments is important. However, the biological interpretation of these changes is problematic. *Gautieria* sporocarp biomass decreased in both treatments, but also decreased in the 15% aggregated retention treatments (D. Luoma, unpublished data; Table 11); no change in *Gautieria* spore frequency was observed in *G. sabrinus* captured in the 15% aggregated retention treatment (Table 5). The number of *G. sabrinus* captured per 100 trap nights decreased in all treatments. The decreases in *G. sabrinus* captures per 100 trap nights in the treatments were significantly different from the decrease observed in the control (C. Maguire and S. West, unpublished data, Tables 9 and 10).

Although similar changes in capture numbers and *Gautieria* sporocarp biomass occurred in the two 40% retention treatments, the response of *Gautieria* spore frequency in the diet of *G. sabrinus* was very different. In the 40% dispersed retention treatment, the frequency of *Gautieria* spores in the diet of *G. sabrinus* significantly increased. As trees are still available as travel routes and are relatively evenly dispersed in this treatment, *G. sabrinus* can continue to move throughout the stand and into adjacent habitat to forage. The relatively large home range (4 – 6 ha) of *G. sabrinus* would allow this animal to forage widely and continue to supplement its diet with *Gautieria* sporocarps despite the decline in biomass in the 40% dispersed retention treatment. The decline in the *G. sabrinus* population in

this treatment would reduce competition for truffles and could be a factor contributing to the increase in *Gautieria* spore frequency in the diet of *G. sabrinus* seen in the 40% dispersed retention treatment. The complication in the interpretation of this increase in *Gautieria* spore frequency arises because no similar response occurred in the 15% dispersed retention treatment.

As *G. sabrinus* may preferentially seek out *Gautieria* truffles, biomass measurements of *Gautieria* sporocarps may underestimate their availability. North *et al.* (1997) demonstrated that in young, managed stands, mean consumption rate of truffles was nearly equal to the standing crop values. Consumption rates of epigeous sporocarps averaged 0.64 kg/ha in all stand types (North *et al.*, 1997). Thus, in the 40% dispersed retention, it is possible that high consumption of *Gautieria* truffles by *G. sabrinus* removed biomass to the point that sporocarps could no longer be detected by the sample. Pre-treatment biomass levels in this treatment were only 0.6 kg/ha.

The sharp decrease in *Gautieria* spore frequency in fecal pellets of *G. sabrinus* from the 40% aggregated retention treatment could be a result of the retention of trees in an aggregated pattern. The reduction in *G. sabrinus* capture numbers means less competition for *Gautieria* sporocarps, but the reduction in *Gautieria* sporocarp biomass in this treatment means that less of the food source is available to the remaining population. The retention of trees in 1 hectare aggregates could severely limit the movement of *G. sabrinus* as travel routes between aggregates and the edge of the treatment are removed. This would limit

the ability of *G. sabrinus* to forage. The decrease in *Gautieria* sporocarp biomass would more strongly affect *G. sabrinus* that have their movement limited by relatively large areas of clearcut, as they can not reach adjacent habitat to supplement their diets. Again, this interpretation of the results is problematic because, although similar responses in *Gautieria* sporocarp biomass and *G. sabrinus* capture numbers occurred in the 15% aggregated retention treatment, no similarly large decrease in *Gautieria* spore frequency in the pellets of *G. sabrinus* occurred. Although a decrease in *Gautieria* spore frequency occurred in the diets of *G. sabrinus* from the 15% aggregated retention treatment, this change was not significantly different from that seen in the control. Additional, unstudied factors and complex interactions among behavioral and biological factors on a broader landscape scale are likely driving much of the observed change in *Gautieria* spore frequency in the diet of *G. sabrinus* in the two 40% retention treatments.

Tamias

The most ubiquitous truffle genus in the diet of the *Tamias* spp. decreased in response to the 15% dispersed retention treatment. This decrease in the frequency of *Rhizopogon* spores in the *Tamias* samples paralleled in the *Rhizopogon* biomass data (D. Luoma, unpublished data; Table 11). The largest decrease in *Rhizopogon* sporocarp biomass occurred in the 15% dispersed retention treatment. The decreases in *Rhizopogon* truffle biomass observed in the 15% aggregated and 40% aggregated retention treatments were not paralleled in the

frequency of *Rhizopogon* spores in the feces of the *Tamias*. A decrease in the number of *Tamias* captured per 100 trap nights occurred in all treatments, and these decreases were significantly different from the decrease in the control (C. Maguire and S. West, unpublished data, Tables 9 and 10). As *Tamias* utilize both forested and non-forested habitat, this animal would be able to travel between aggregates to seek out truffles. This helps to explain the lack of a significant shift in *Rhizopogon* spore frequency in the diet of *Tamias* from the two aggregated retention treatment despite the decrease in *Rhizopogon* sporocarp biomass observed. The ability to use multiple microhabitats in the DEMO treatments probably allowed this animal to continue to seek out sufficient amounts of *Rhizopogon* truffles for its diet despite decreases in truffle biomass. Only in the treatment where *Rhizopogon* sporocarp biomass showed a very substantial decrease, did the frequency of *Rhizopogon* spores in the diet reflect a decrease.

As *Rhizopogon* is the most ubiquitous spore in the diet of all three animal genera studied, competition among animal genera for this truffle genus may be intense. Animals with limited home ranges and habitat requirements, such as *Clethrionomys*, may be more affected by intergeneric competition for *Rhizopogon*. *Tamias* has a similar home range size as *Clethrionomys* (Carey, 1991), but wider habitat requirements. Thus, *Tamias* may be able to better compete for *Rhizopogon* truffles by traveling across multiple microhabitats.

Total cumulative number of genera

Genera accumulation curves constructed for this research indicated that a minimum of 8 animals was generally sufficient to observe the majority of the truffle genera available to be eaten by the study animals. This is similar to the number obtained by Carey *et al.* (1999) as adequate to estimate genus richness in the diets of flying squirrels and chipmunks.

No treatment effect was evident for the change in the mean total cumulative number of genera in the diet of *G. sabrinus* ($p = 0.1906$) or the *Tamias* species ($p = 0.6664$) (Tables 5 and 7). As *G. sabrinus* is most heavily reliant upon a varied diet of truffles and if the movements of *G. sabrinus* were limited by the aggregation of remaining trees, a decrease in the number of genera in the diet of *G. sabrinus* in the aggregated treatments would be expected. Based on the cumulative number of genera analysis, the remaining *G. sabrinus* were able to compensate for the decrease or loss in the abundance of any truffle genera in the treatments, perhaps by altering their behavior. However, as previously mentioned, the genera accumulation curves for certain block x treatment x condition combinations for *G. sabrinus* did not approach the asymptote, potentially limiting the ability of this study to adequately measure the change in the total cumulative number of genera in the diet of *G. sabrinus* in all treatments. However, the smaller number of genera measured in several combinations would result in a Type I error, as the pre- and post-treatment differences would actually be greater than measured. Therefore, it

can be assumed that no actual change in the mean total cumulative number of genera occurred in the diet of *G. sabrinus*.

If *Tamias* actively seek out truffles, the low frequency of truffle spores (except for the genus *Rhizopogon*) in the diet of the *Tamias* spp. suggests that a substantial decrease in the biomass of the common truffle genera would have to occur for a decrease in the number of genera in the diet of the *Tamias* spp. Additionally, the ability of the *Tamias* spp. to travel in both forested and non-forested habitat would enable these animals to continue to seek truffles in forested areas separated by clearcuts. The *Tamias* genera accumulation curves, like the *G. sabrinus* genera accumulation curves, did not approach the asymptote in all block x treatment x condition combinations. This potentially limited the ability of the analysis to adequately measure the change in the total cumulative number of genera in all treatments. Again, the reduced number of genera measured in the pre-treatment *Tamias* diets would make pre- and post-treatment differences greater, resulting in a possible failure to accept the null hypothesis.

The mean total cumulative number of genera found in the diet of the *Clethrionomys* species changed in response to the application of treatments ($p = 0.0289$; Table 3). *Clethrionomys* captured in the 40% dispersed retention unit showed a statistically significant decrease ($p = 0.0278$) in the cumulative number of genera in their diets after treatments were applied compared to the change in the number of genera in the control. In all other treatments, the cumulative number of genera in the diet of the *Clethrionomys* spp. increased. Biological interpretation of

this decrease in the mean total cumulative number of genera is problematic. No clear connection between this retention treatment and the cumulative number of genera in the diet of *Clethrionomys* is evident. Complex biological interactions involving interspecific competition or other factors not measured in this study may be influencing this result. Additionally, this significant result may be a Type I error, given the number of comparisons made in this study and the limited replication.

CONCLUSIONS

It was concluded that:

1)   The pre-treatment diets of the study animals differed significantly among genera. The diet of the *Tamias* spp. contained a greater frequency of plant material than the diet of the *Clethrionomys* or *Glaucomys*. *Gautieria* and *Leucogaster* spores were present at higher frequencies in the diet of *Glaucomys* than either of the other two animal genera. *G. sabrinus* samples contained the highest mean number of genera per sample. Spores of the most common truffle genera were more consistently present and at higher frequencies in the diet of *Glaucomys sabrinus* than the diet of the *Clethrionomys* or the *Tamias*.

2)   The mean total cumulative number of truffle genera in the diet of the study animals showed little change. Only in the diet of *Clethrionomys* in the 40% dispersed retention treatment was a significant change detected. *Clethrionomys* captured in treatments with less green-trees retained did not show a greater change in the number of truffle genera in the diet as hypothesized. The cumulative number of genera in the diets of *Glaucomys* and *Tamias* spp. did not show a significant change as a result of the application of treatments.

3)   The frequencies of the spores of the most common truffle genera in

the diets of the study animals showed a significant change in some

treatments. The harvesting of trees appears to negatively affect the

frequency of *Rhizopogon* spores in the diet of the *Clethrionomys*

spp., potentially reflecting the reduced ability of these animals to

forage for *Rhizopogon* truffles and a reduction in *Rhizopogon*

abundance or frequency. The retention of trees in isolated

aggregates restricts the movement of *Clethrionomys* within the

treatments, and the abundance of edge may further restrict

Clethrionomys to the center of an aggregate. Competition would be

increased within these aggregates where animals are concentrated

and the resource may be even more limited.

The retention of trees in aggregates may limit the ability of

G. sabrinus to move and forage between aggregates and into

adjacent habitat. However, in the dispersed retention treatments,

adequate travel routes are still available and *G. sabrinus* could

forage throughout the treatment and in to adjacent habitat, thus

reducing the impact of the reduction of truffle biomass within a

stand.

The diet of the *Tamias* spp. showed little change in response

to the treatments. The wide diversity of habitats that *Tamias* utilize

may extend the ability of this animal to find and compete for truffles

even as they decreased locally, until a large decrease in biomass occurred.

The sporocarp biomass data (D. Luoma, unpublished data) showed that overall truffle biomass declined, whereas consumption of truffles by these small mammals largely stayed the same. This suggests that the animals are compensating for a locally declining food source by altering their foraging behavior. The long term effects of this behavioral compensation on energetics and population dynamics is unknown.

SUMMARY

This study was part of the Demonstration of Ecosystems Management Options (DEMO) study, a long-term project designed to examine the effects of different levels and patterns of green-tree retention on multiple forest attributes. For this study, the effect of six different retention levels and patterns on the diets of squirrels, chipmunks, and voles was examined. The diets of five species from these animal groups were examined: *Glaucomys sabrinus*, *Tamias townsendii*, *Tamias siskiyou*, *Clethrionomys californicus*, and *Clethrionomys gapperi*. *Glaucomys* and *Tamias* diet data was collected from two of the DEMO blocks, and *Clethrionomys* diet data was collected from four of the blocks.

Fecal pellet analysis was used as a non-lethal method of examining the diets of these mycophagous animals. This methodology allows examination of an animal's recent meals. Data was collected both prior to the harvesting of trees (pre-treatment), and after the trees were harvested (post-treatment). Pre-treatment diet data was utilized for a diet comparison among the animal genera. To detect treatment effects, change in the frequencies of the most common truffle genera and plant material and the total cumulative number of truffle genera in the diet was calculated from the post-treatment and pre-treatment diet data. These changes in the frequency or cumulative number of genera were examined for a treatment effect.

The comparison among the pre-treatment diets of the study animals showed a strong difference among animal genera. *G. sabrinus* fecal samples contained higher frequencies of *Gautieria* and *Leucogaster* spores than fecal samples from *Clethrionomys* or *Tamias*. *G. sabrinus* samples contained the highest mean number of genera per sample and consistently had high mean frequencies for several fungal genera. *Clethrionomys* samples often contained a high number of truffle genera as well, and commonly had moderately high mean frequencies for several genera. *Tamias* samples contained a significantly higher frequency of plant material than either *Glaucomys* or *Clethrionomys* samples. The frequency of *Rhizopogon* spores was consistently > 95% in the diet of all animal genera.

This study has supported the conclusion by other researchers that the northern flying squirrel (*G. sabrinus*) consumes *Gautieria* truffles more frequently than either chipmunks or voles and perhaps preferentially (Colgan *et al.*, 1997; Zabel and Waters, 1997; Cázares *et al.*, 1999) and that *G. sabrinus* is a fungal specialist (Maser *et al.*, 1986; Carey *et al.*, 1999; Claridge *et al.*, 1999). The high frequency of plant material in the diet of the *Tamias* in this study emphasized the more varied diet of this animal genus as compared to either *G. sabrinus* or *Clethrionomys* spp.

The mean total cumulative number of genera in the diet of *G. sabrinus* or the *Tamias* spp. did not show a treatment effect. Both of these animal genera may be able to travel further to forage for truffles than the *Clethrionomys* spp; *G. sabrinus* has a much larger home range and its diet may not be as affected by

localized thinning. The *Tamias* spp. utilize a wider variety of habitats, enabling them to forage across clearcuts. A treatment effect was evident for the *Clethrionomys* samples in the 40% dispersed retention treatment, declining by a mean 1.0 genera. Complex biological factors other than solely removal of trees in the 40% dispersed retention treatment may have caused this decrease in the mean total cumulative number of genera in the diet of *Clethrionomys*.

A treatment effect was evident for at least one truffle genus spore frequency in the diet of each animal genus. The frequency of *Rhizopogon* spores in the diet of the *Clethrionomys* significantly decreased in the 75% aggregated, 40% dispersed, 40% aggregated, and 15% aggregated retention treatments compared to the change in *Rhizopogon* spore frequency observed in the diet of *Clethrionomys* captured in the control. It is apparent that, for *Clethrionomys*, the harvesting of trees negatively affects the frequency of *Rhizopogon* spores in the diet, potentially reflecting the reduced ability of these animals to forage for *Rhizopogon* and a reduction in *Rhizopogon* truffle abundance. The greatest decrease in *Rhizopogon* spore frequency was observed in the 15% aggregated retention treatment, indicating that the retention of trees in an isolated aggregated pattern affects the frequency of *Rhizopogon* spores in the diet of the *Clethrionomys*. The majority of the *Clethrionomys* captured in the aggregated retention treatments were captured in the forest aggregates. An island effect and possibly a negative edge effect in the aggregated retention units could be decreasing the ability of *Clethrionomys* to

forage for *Rhizopogon* truffles or decreasing the access to these truffles, while locally increasing competition.

Gautieria spore frequency decreased in the diet of *Glaucomys sabrinus* in the 40% aggregated retention treatment and increased in the 40% dispersed retention unit. As this truffle may be preferentially eaten by *G. sabrinus*, a change in the spore frequency in the diet may be indicative of an animal's ability to detect *Gautieria* truffles or a change in the abundance of these truffles. Simple treatment effects related to change in truffle biomass production are inadequate to explain the observed dietary changes. In the 40% aggregated retention treatment, the retention of trees in isolated aggregates limits the movement and foraging ability of *G. sabrinus*. The decrease in *Gautieria* truffle biomass in this treatment combined with the reduced ability of *G. sabrinus* to forage for its favorite truffle, could increase competition for *Gautieria* truffles despite the reduction in *G. sabrinus* captures per 100 trap nights. However, no similar effect on *Gautieria* spore frequency in the diet of *G. sabrinus* was found in the 15% aggregated retention treatment. In the 40% dispersed retention treatment, *G. sabrinus* may continue to travel throughout the treatment and into adjacent habitat to forage for truffles. Thus, although *Gautieria* biomass showed a decline in this treatment, the reduced competition for truffles due to the reduction in *G. sabrinus* numbers and the ability to forage into adjacent habitat may account for the increase in *Gautieria* spore frequency in the diet of *G. sabrinus* from this treatment. Alternately, the biomass

measurement of *Gautieria* truffles may underestimate *Gautieria* availability to *G. sabrinus* due to a high consumption rate of this truffle by *G. sabrinus*.

A treatment effect was evident for the change in frequency of *Rhizopogon* spores in the diet of the *Tamias* in the 15% dispersed retention treatment. In the feces of animals captured in this treatment, the frequency of *Rhizopogon* spores significantly decreased compared to the change in spore frequency seen in fecal samples from the control. Because *Tamias* are able to travel between forested and non-forested habitat, the pattern of tree retention should not strongly affect the foraging behavior of this animal. The wide diversity of habitats that *Tamias* utilizes may increase its ability to find *Rhizopogon* truffles even as truffles decrease locally and interspecific competition for this resource increases, except when a large and widespread decrease in biomass occurs.

The replication for the *Tamias* and *Glaucomys* data was minimal, limiting confident extrapolation of the results to a larger scale. However, for this study, the diets of hundreds of these animals were examined. The *Clethrionomys* data was collected from four of the DEMO blocks and the diets of over a thousand animals were examined. Thus, the results from the *Clethrionomys* data may be extrapolated to Douglas-fir forests of the Pacific Northwest with greater confidence.

Forest managers should expect that in predominately Douglas-fir forests of the Pacific Northwest, the harvesting of trees will reduce the consumption of *Rhizopogon* in the diet of *Clethrionomys californicus* and *C. gapperi*. *Rhizopogon* truffles are an important food source for many small mammals, and are an

ectomycorrhizal associate of Douglas-fir. It is probable that the decline in *Rhizopogon* spore frequency in the diets of the *Clethrionomys* reflects a large decrease in the availability or accessibility of *Rhizopogon* truffles, especially in the 15% aggregated retention. Over the long term, this reduction in *Rhizopogon* spore frequency in the diets of the *Clethrionomys* spp. could translate into a reduced dispersal of spores and a further reduction in *Rhizopogon* truffle biomass and abundance. If this important truffle greatly declines in availability, the abundance of other small mammals may decrease in response. In order to preserve this important food source and ensure adequate *Rhizopogon* spore dispersal, forest managers should consider refraining from retaining green-trees in isolated aggregates. Tree harvests that include aggregates within a dispersed retention matrix would enable mycophagous small mammals that avoid areas devoid of trees to continue dispersal of *Rhizopogon* spores.

Overall, small mammal consumption of truffles showed little change in response to the treatments. Although overall truffle biomass declined (D. Luoma, unpublished data), and small mammal populations changed (C. Maguire and S. West, unpublished data), truffle consumption of the common genera was relatively unchanged. This suggests that the harvesting of trees is forcing some behavioral change on these animals, causing them to forage further or enter unsuitable habitat to find adequate amounts of truffles. There may be long term effects on animal energetics and populations dynamics resulting from this behavioral shift.

Future research involving the effect of tree removal on the diets of mycophagous small mammals should ensure the presence of the animals of interest with adequate replication of treatments across the landscape. That will expand the scale of inference across which the results are applicable. Sampling small mammal diets across more seasons should also be done to detect effects that are more evident as competition for this limited resource (truffles) increases during periods of low production. Additionally, truffle production is highly seasonal by species (Luoma *et al.*, 1991) and the various species may be affected by treatments differently.

An additional response variable may improve the quantification of small mammal mycophagy. The response variable used in this study, presence out of a possible 75 fields, did not account for the absolute abundance of spores within those fields. Thus, one spore in a field-of-view was considered to be equal to one thousand spores in a field-of-view when accounting for presence. Williams (1987) discusses two methods of density estimation for plant material. His method 2, where a limited number of fields on a slide are observed and density is "given in terms of the number of particles per unit" is similar to what is suggested below. However, given the small size of fungal spores, Williams' procedure would have to be performed at higher magnifications or with various sample concentrations, as it still relies on a presence/absence in a field-of-view calculation. Thus, at high sample concentrations, the density of spores present in all fields-of-view can not be calculated without further dilution and sampling. The following procedure could

account for large differences in absolute spore numbers among genera while at the same time estimating density in the traditional terms of frequency: slides would be prepared as in the methods in this study. First, examine representative samples as in this study, to determine the common fungal genera. Then, 25 fields per cover slip (for three cover slips) would be examined at 400x magnification with a gridded ocular. For the common genera in the diet of the animals under study, estimate the percent of the grid covered by the spore type of each truffle genus. An average density is calculated from the 75 fields-of-view by visually estimating the percent of the grid in each field covered by the spores of a genus and then averaging these values across the 75 fields. Truffle genera other than the most common spore types would continue to be counted as present or absent in a field-of-view. This procedure should provide better estimates of the relative importance of the most abundant food items (i.e. *Rhizopogon*) that currently are underestimated when values approach 100%. Changes in spore abundance in fecal pellets should be more readily detected.

LITERATURE CITED

Alexander, L. F., and B. J. Verts. 1992. *Clethrionomys californicus.* Mammalian Species 406:1-6.

Alexopoulus, C.J., C.W. Mims, and M. Blackwell. 1996. Introductory Mycology. John Wiley and Sons, New York.

Amaranthus, M., J.M. Trappe, L. Bednar, and D. Arthur. 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 Forestry Research 24:2157-2165.

Ashton, D.H. 1976. Studies on the mycorrhizae of *Eucalyptus regnans* F. Muell. Australian Journal of Botany 24:723-741.

Aubry, K.B., M.P. Amaranthus, C.B. Halpern, J.D.White, B.L. Woodard, C.E.Peterson, C.A. Lagoudakis, and A.J. Horton. 1999. Evaluating the effects of varying levels and patterns of green-tree retention: experimental design of the DEMO study. Northwest Science 73 (Spec. Iss): 12-26.

Bennett and Byrony. 1997. (Autumn) Fungi, fast food of the forest. Ecosystems 91:36.

Blaschke, H., and W. Bäumler. 1989. Mycophagy and spore dispersal by small mammals in Bavarian forests. Forest Ecology and Management 26:237-245.

Bowman, J.C., D. Sleep, G.J. Forbes, and M. Edwards. 2000. The association of small mammals with coarse woody debris at log and stand scales. Forest Ecology and Management 129:119-124.

Carey, A. B. 1991. The biology of arboreal rodents in Douglas-fir forests. USDA Forest Service, General Technical Report PNW-276. Portland, Oregon, USA.

Carey, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648-661.

Carey, A.B., W. Colgan III, J.M. Trappe, and R. Molina. 2002. Effects of forest management on truffle abundance and squirrel diets. Northwest Science, in press.

Carey, A. B., J. Kershner, B. Biswell, and L. Dominguez de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142:1-71.

Castellano, M.A., J.M. Trappe, Z. Maser, and C. Maser. 1989. Key to Spores of the Genera of Hypogeous Fungi of North Temperate Forests with Special Reference to Animal Mycophagy. Mad River Press. Eureka, California.

Catalfamo, J., and J.M. Trappe. 1970. Ectomycorrhizal Fungi: A Phytochemical Survey. Northwest Science 44:19-24.

Cázares, E., and J.M. Trappe. 1994. Spore dispersal of ectomycorrhizal fungi on a glacier forefront by mammal mycophagy. Mycologia 86(4):507-510.

Cázares, E., D.L. Luoma, J.L. Eberhart, M.P. Amaranthus, C. Cray, M.P. Dodd, and M. McArthur. 1998. Hypogeous fungal diversity and biomass following salvage logging in Mt. Hood National Forest, Oregon, USA. Abstracts. Second International Conference on Mycorrhizae. Uppsala, Sweden. pp. 39-40.

Cázares, E., D.L. Luoma, M.P. Amaranthus, C.L. Chambers, and J.F. Lehmkuhl. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade range. Northwest Science 73 (Special Issue):64-76.

Claridge, A.W., and D.B. Lindenmayer. 1998. Consumption of hypogeous fungi by the mountain brushtail possum (*Trichosurus caninus*) in eastern Australia. Mycological Research 102(3):269-272.

Claridge, A.W., M.T. Tanton, J.H. Seebeck, S.J. Cork, and R.B. Cunningham. 1992. Establishment of ectomycorrhizae on roots of two species of eucalyptus from fungal spores contained in the faeces of the long-nosed potoroo (*Potorous tridactylis*). Australian Journal of Ecology 17:207-217.

Claridge, A.W., J.M. Trappe, S.J. Cork, and D.L. Claridge. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. Journal of Comparative Physiology. B:Biochemical, Systematic, and Environmental Physiology 169:172-178.

Clarkson, D.A., and L.S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68(4):259-265.

Colgan III, W., A. B. Carey, and J. M. Trappe. 1997. A reliable method of analyzing dietaries of mycophagous small mammals. Northwest Naturalist 78:65–69.

Colgan III, W., A.B. Carey, J.M.Trappe, R. Molina, and D. Thysell. 1999. Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. Canadian Journal of Forest Research 29: 1259-1268.

Colwell, R.K. 1997. EstimateS version 5.0.1.

Cooper, K.M. 1975. Growth responses to the formation of endotrophic mycorrhizas in Solanum, Leptospermum, and New Zealand ferns. In: Endomycorrhizas: proceedings of a symposium held at the University of Leeds. (eds. F.E. Sanders, B. Mosse, and P.B. Tinker). Academic Press. pp. 391-407.

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

Donaldson, R., and M. Stoddart. 1994. Detection of hypogeous fungi by Tasmanian bettong (*Bettongia gaimardi*: Marsupialia: Macropodoidea). Journal of Chemical Ecology 20:1201-1207.

Duchesne, L.C. 1994. Role of ectomycorrhizal fungi in biocontrol. In: Mycorrhizae and plant health. (eds. F.L. Pfleger and R.G. Linderman). APS Press, St. Paul, Minnesota. pp. 27-45.

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

Fogel, R., and J.M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science 52(1):1-31.

Foresman, K.R. 2001. The Wild Mammals of Montana. American Society of Mammalogists, Special Publication #2.

Forsman, E.D., E.C. Meslow, and H.M. Wight. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs 87: 64 pp.

Forsman, E.D., I.A. Otto, S.G. Sovern, M.G. Taylor, D.W. Hays, H. Allen, S.L. Roberts, and D.E. Seaman. 2001. Spatial and temporal variation in diets of spotted owls in Washington. Journal of Raptor Research. 35(2)141-150.

Franklin, J.F. and D.S. DeBell. 1973. Effects of various harvesting methods on forest regeneration. In: Proceedings of the Symposium on Even-age Management, August 1, 1972 (eds. R.K. Hermann and D.P. Lavender). School of Forestry, Oregon State University. pp. 29 – 57.

Gashwiler, J.S. 1967. Conifer seed survival in a western Oregon clearcut. Ecology 48:431-438.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west central Oregon. Ecology 51:1018-1026.

Getz, L.L. 1968. Influence of water balance and microclimate on the local distribution of the red-backed vole and white-footed mouse. Ecology 49:276-286.

Gomez, unpublished data on file with Oregon Cooperative Wildlife Research Unit.

Grönwall, O., and A. Pehrson. 1984. Nutrient content in fungi as a primary food of the red squirrel, *Sciurus vulgaris* L. Oecologia 64:230-231.

Gurnell, J. 1987. Natural History of Squirrels. Facts on File Publications, New York, New York.

Hall, E.R. 1981. The Mammals of North America, Vol 1 2nd ed. John Wiley and Sons, New York, New York. USA.

Halpern, C.B., and T.A. Spies. 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecological Applications 5:914-934.

Halpern, C.B., S.A. Evans, C.R. Nelson, D. McKenzi, D.A. Ligouri, D.E. Hibbs, and M.G. Halaj. 1999. Response of forest vegetation to varying levels and patterns of green-tree retention: an overview of a long-term experiment. Northwest Science 73 (Spec. Iss.): 27-44.

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

Hastings, S., and J.C. Mottram. 1916. Observations upon the edibility of fungi for rodents. Transactions of the British Mycological Society 5:364-378.

Hayes, J.P, S.P. Cross, and P.W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northwest Science 60:250-256.

Hayes, J.P, E.G. Horvath, and P. Hounihan. 1995. Townsend's chipmunk populations in Doug-fir plantations and mature forests in the Oregon coast range. Canadian Journal of Zoology 73:67-73.

Horn, B.S., and G.D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57:32-44.

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

Kleinschmidt, G.D., and J.W. Gerdemann. 1972. Stunting of citrus seedlings in fumigated nursery soils related to the absence of endomycorrhiza. Phytopathology 62:1447-1453.

Kotter, M.M., and R.C. Farentinos. 1984. Formation of ponderosa pine ectomycorrhizae after inoculation with feces of tassel-eared squirrels. Mycologia 76(4): 758-760.

Lamont, B.B., C.S. Ralph, and P.E.S. Christensen. 1985. Mycophagous marsupials as dispersal agents for ectomycorrhizal fungi on *Eucalyptus calophylla* and *Gastrolobium bilobum*. New Phytologist 101:651-656.

Lehmkuhl, J.F., S.D. West, C.L. Chambers, W.C. McComb, D.A. Manuwal, K.B. Aubry, J.L. Erickson, R.A. Gitzen, and M. Leu. 1999. Assessing wildlife response to varying levels and patterns of green-tree retention in western Oregon and Washington. Northwest Science 73:45-63.

Luoma, D.L. 1988. Biomass and community structure of sporocarps formed by hypogeous ectomycorrhizal fungi within selected forest habitat of the H.J. Andrews experimental forest. Ph.D. Thesis, Oregon State University, Corvallis, Oregon, USA.

Luoma, D.L. 1991. Annual changes in seasonal production of hypogeous sporocarps in Oregon Douglas-fir forests. In: Wildlife habitat relationships in old-growth Douglas-fir forests. (technical coordinators: L.F. Ruggiero, K.B. Aubry, A.B. Carey, and M.H. Huff) USDA Forest Service, Gen. Tech. Report PNW-GTR-285. Portland, Oregon, USA. Pages 83-89.

Luoma, D.L., R.E. Frenkel, and J.M. Trappe. 1991. Fruiting of hypogeous fungi in Oregon Douglas-fir forests: seasonal and habitat variation. Mycologia 83:335-353.

Luoma, D.L. Unpublished data on DEMO sporocarp production.

Maguire, C., and S. West. Unpublished data on DEMO small mammal captures.

Malajczuk, N., J.M. Trappe, and R. Molina. 1987. Interrelationships among some ectomycorrhizal trees, hypogeous fungi, and small mammals: Western Australian and northwestern American parallels. Australian Journal of Ecology 12:53-55.

Marin, A.B., and M.R. McDaniel. 1987. An examination of hedonic responses to *Tuber gibbosum* and three other native Oregon truffles. Journal of Food Science 52:1305-1307.

Martin, K.J. 1994. Movements and habitat associations of northern flying squirrels in the central Oregon Cascades. M.S. Thesis, Oregon State University. Corvallis, Oregon. 46 pp.

Martin, K. J., and Anthony, R. G. 1999. Movements of northern flying squirrels in different-aged forest stands of western Oregon. Journal of Wildlife Management 63:291-297.

Marx, D.H. 1973. Mycorrhizae and feeder root diseases. In: Ectomycorrhizae: Their Ecology and Physiology (eds. G.C. Marks and T.T. Kozlowski). Academic Press, New York, USA. pp. 351-382.

Maser, C., and Z. Maser. 1988a. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Naturalist 48:358-369.

Maser, C., and Z. Maser. 1988b. Mycophagy of red-backed voles, *Clethrionomys californicus* and *C. gapperi*. Great Basin Naturalist 48(2):269-273.

Maser, Z., C. Maser, and J.M. Trappe. 1985. Food habits of northern flying squirrel (Glaucomys sabrinus) in Oregon. Canadian Journal of Zoology 63:1084-1088.

Maser, C., Z. Maser, J.W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology 64:2086-2089.

Maser, C., Z. Maser, and R. Molina. 1988. Small-mammal mycophagy in rangelands of central and southeastern Oregon. Journal of Range Management 41(4):309-312.

Maser, C., J.M. Trappe, and R.A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59(4):799-809.

Massicotte, H.B., R.L. Peterson, C.A. Ackerly, and Y. Piché. 1986. Structure and ontogeny of *Alnus crispa-Alpova diplophloeus* ectomycorrhizae. Canadian Journal of Botany 64:177-192.

Massicotte, H.B., R.L. Peterson, C.A. Ackerly, and L.H. Melville. 1990. Structure and ontogeny of Betula alleghaniensis-Pisolithus tinctorius ectomycorrhizae. Canadian Journal of Botany 68:579-503.

McIntire, P. W. 1984. Fungus consumption by the Siskiyou chipmunk within a variously treated forest. Ecology 65:137-149.

McIntire, P.W. and A.B. Carey. 1989. A microhistological technique for analysis of food habits of mycophagous rodents. USDA Research Paper PNW-RP-404.

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

Miller, H.A., and L.K. Halls. 1969. Fleshy fungi commonly eaten by southern wildlife. USDA Forest Service, Research Paper SO-49. New Orleans, Louisiana, USA.

Miller, H.A., P. Torres, and T.M. McClean. 1994. Persistence of basidiospores and sclerotia of ectomycorrhizal fungi and *Morchella* in soil. Mycologia 86:89-95.

Mills, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conservation Biology 9:395-403

North, M., J.M. Trappe, J. Franklin. 1997. Standing Crop and animal consumption of fungal sporocarps in PNW forests. Ecology 78(5):1543-1554.

Perez Calvo, J.G., Z. Maser, and C. Maser. 1989. Note on fungi in small mammals from the Nothofagus forests in Argentina. Great Basin Naturalist 49(4):618-620.

Pyare, S., and W.S. Longland. 2001a. Mechanisms of truffle detection by northern flying squirrels. Canadian Journal of Zoology 79:1007-1015.

Pyare, S., and W.S. Longland. 2001b. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681-689.

Rhoades, F. 1986. Small mammal mycophagy near woody debris accumulations in the Stehekin River Valley, Washington. Northwest Science 60(3):150-153.

Ribe, R. 1999. Regeneration harvests versus clearcuts: public views of the acceptability and aesthetics of Northwest Forest Plan harvests. Northwest Science 73:102-117.

Rogerson, T.L. 1976. Soil water deficits under forested and clearcut areas in northern Arkansas. Soil Science Society of America Journal 40: 802-805.

Rosenberg, D.K. 1990. Characteristics of northern flying squirrel and Townsend's chipmunk populations in second- and old-growth forests. M.S. Thesis, Oregon State University, Corvallis Oregon, USA.

Rosenberg, D. K., and R. G. Anthony. 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, D.K., K. Swindle, and R.G. Anthony. 1994. Habitat associations of California red-backed voles in young and old-growth forests of western Oregon. Northwest Science 68: 266-272.

SAF. 2002. http://www.safnet.org/archive/clearcut.htm. Society of American Foresters website.

Shemakhanova, N.M. 1967. Mycotrophy of Woody Plants. Israel Program for Scientific Translations, Jerusalem. US Dept of Commerce TT 66-51073. 329 pp.

Smith, C.C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. Journal of Wildlife Management 32 2:305-317.

Smith, S.E., and D.J. Read. 1997. Mycorrhizal symbiosis. Academic Press, London, England.

Smith, J.E., R. Molina, M.M.P. Huso, D.L. Luoma, D. McKay, M.A. Castellano, T. Lebel, and Y. Valachovic. 2002. Species richness, abundance, and composition of hypogeous and epigeous ectomycorrhizal fungal sporocarps in young, rotation-age, and old-growth stands of Douglas-fir (Pseudotsuga menziesii) in the Cascade Range of Oregon, USA. Canadian Journal of Botany 80:186-204.

Stark, N. 1972. Nutrient cycling pathways and litter fungi. Bioscience 22:355-360.

Stark, N.M. 1979. Nutrient losses from timber harvesting in a larch/Douglas-fir forest. USDA Forest Service Research Paper. INT-231. 41 pp.

States, J.S., and W.S. Gaud. 1997. Ecology of hypogeous fungi associated with ponderosa pine. I. Patterns of distribution and sporocarp production in some Arizona forests. Mycologia 89:712-721.

Stockdale, C. 2000. Green-tree retention and ectomycorrhiza legacies: the spatial influences of retention trees on mycorrhiza community structure and diversity. M.S. Thesis, Oregon State University, Corvallis, Oregon, USA.

Sullivan, T.P., R.A. Lautenschlager, and R.G. Wagner. 1999. Clearcutting and burning of northern spruce-fir forests, implications for small mammal communities. Journal of Applied Ecology 36: 327-344.

Sutton, D.A. 1993. Tamias townsendii. Mammalian Species 435:1-6.

Taylor, P. 2000. Major player. National Wildlife. 38:46-51.

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

Tevis, L., Jr. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy 34:3L6-324.

Thiers, H.D. 1984. The secotioid syndrome. Mycologia 76:1-8.

Thompson, R.L. 1996. Home range and habitat use of western red-backed voles in mature coniferous forests in the Oregon Cascades. M.S. Thesis. Oregon State University, Corvallis, Oregon, USA.

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

Trappe, J.M., and R.D. Fogel. 1977. Ecosystematic functions of mycorrhizae. In The belowground ecosystem: a synthesis of plant-associated processes. Range Science Dep. Sci. Ser. No. 26, U.S.D.A. Forest Service, Fort Collins.

Trappe, J.M., and D.L. Luoma. 1992. Chapter 2. The ties that bind: Fungi in ecosystems. In G.C. Carroll and D.T. Wicklow (eds.) The fungal community: Its organization and role in the ecosystem. Second edition. Marcel Dekker, Inc. New York. pp.17-27.

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

Trappe, J.M., and C. Maser. 1977. Ectomycorrhizal fungi: interactions of mushrooms and truffles with beasts and trees. In T. Walters (ed.) Mushrooms and man, an interdisciplinary approach to mycology. U.S.D.A. Forest Service. pp. 165-179.

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

US Department of Agriculture, Forest Service; US Department of the Interior, Bureau of Land Management. 1994. Final Supplemental Environmental Impact Statement on Management of Habitat for Late-successional and Old-growth Forest Related Species Within the Range of the Spotted Owl. Vol. 1, US Department of Agriculture, Forest Service, US Department of the Interior, Bureau of Land Managmenet: Washington, DC.

Van Horne, B., R.L. Schooley, and P.B. Sharpe. 1998. Influence of habitat, sex, age, and drought on the diet of Townsend's ground squirrels. Journal of Mammalogy 79(2):521-537.

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

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

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

Wells-Gosling, N. 1985. Flying squirrels: gliders in the dark. Smithsonian Institute Press.

Wells-Gosling, N., and L.R. Heaney. 1984. Glaucomys sabrinus. Mammalian Species 229:1-8.

Williams, B.K. 1987. Frequency sampling in microhistological studies: an alternative model. Journal of Range Management 40(2):109-112.

Witt, J.W. 1992. Home range and density estimates for the northern flying squirrel, Glaucomys sabrinus, in western Oregon. Journal of Mammalogy 73:921-929.

Zabel, C.J., and J.R. Waters. 1997. Food preferences of captive northern flying squirrels from the Lassen National Forest California. Northwest Science 71(2):103-107.

Zabel, C. J., K. McKelvey, and J.P. Ward Jr. 1995. Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). Canadian Journal of Zoology 73:433-439.