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Seasonal Variation in Mycophagy by the Western Red-backed Vole, *Clethrionomys californicus*, in Southwestern Oregon

Abstract

We analyzed the fungal spore content of fecal pellets collected from western red-backed voles (*Clethrionomys californicus*) live-trapped between 1981 November and 1982 November in the foothills of the Cascade Range of southwestern Oregon. Nineteen fungal genera were identified, 17 of which were hypogeous mycobionts. *Rhizopogon* was the most frequently occurring genus. Statistically significant temporal variation occurred in spore abundance, number of genera per sample, and the relative abundance of each genus. Maximum fungus consumption occurred during late summer. Variation in mycophagy appears to be associated with seasonal changes in sporocarp abundance. Western red-backed voles apparently are hypogeous fungal generalists, foraging on sporocarps in direct relation to their availability.

Introduction

Until recently, little has been known about the food habits of the western red-backed vole (*Clethrionomys californicus*). Maser and Storm (1970) reported that *Clethrionomys* stomach contents consisted of finely chewed green material. Maser *et al.* (1978a) provided the first quantitative analysis of western red-backed vole stomach contents. They found that this species is highly mycophagous (fungus-eating), with 68 percent of the stomach contents by volume consisting of fungi. The majority of the identified fungi were hypogeous (below ground) fruiters; i.e. truffles and their relatives. Ure and Maser (1982) examined the stomach contents of two subspecies of *C. californicus* and three subspecies of *C. gapperi*. They found that *C. californicus* fed heavily on fungal sporocarps and lichens, and that the degree of mycophagy at higher elevations varied seasonally.

Small mammal mycophagy has important implications to forest management (Maser *et al.* 1978b). The majority of fungi eaten by the red-backed vole are ectomycorrhizal (Ure and Maser 1982). Mycorrhizal fungi form a symbiosis with vascular plant roots. Woody plants depend on

mycorrhizae for adequate nutrient uptake. Mycorrhizae also increase longevity, size, and respiration rate of their host's roots and protect feeder roots against pathogens (Trappe and Fogel 1977). Hypogeous mycorrhizal fungi depend on mycophagy for spore dispersal (Trappe and Maser 1977, Maser *et al.* 1978b). Although the potential importance of spore dispersal by small mammals was noted over 30 years ago (Tevis 1952), its implications to forest management have not been widely recognized.

Although old-growth forests provide optimal habitat for the western red-backed vole (Tevis 1956, Gashwiler 1977, Franklin *et al.* 1981), red-backed voles occasionally occur in logged habitats if suitable microhabitats are maintained (Hayes 1983). The absence of *C. californicus* from clearcuts (Gashwiler 1959, 1970; Hayes 1983; Hooven and Black 1976) negates any significant role of this species as effective vectors of mycorrhizal fungal spores in clearcuts, but *C. californicus* may aid reforestation efforts through dispersal of spores in less disturbed logged habitats. Movements between suitable microhabitats could result in the dispersal of fungal spores into adjacent logged habitats.

We analyzed the spore content of feces from western red-backed voles captured over a 13-month period to examine seasonal variation in mycophagy. The analysis provides data on the

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amount and types of fungal spores transported via feces, the relative temporal variation in mycophagy, and phenology of hypogeous sporocarps.

Study Area

The study area is at ca. 900 m elevation in the foothills of the southern Cascade Range, Jackson County, 23 km northeast of Ashland, Oregon, T37S, R3E, Sections 19 and 20, Willamette Meridian. The slope ranges from 0° to over 35° with a predominantly east-facing aspect. Soda Creek, a small perennial stream, runs 40 to 100 m east of the study area.

The region is characterized by relatively mild, wet winters and hot, dry summers. Night temperatures are often low, and may drop below 0°C at upper elevations during summer.

The vegetation of the study area is old-growth forest in the mixed conifer zone (Franklin and Dyrness 1973). Douglas-fir (*Pseudotsuga menziesii*) is the most abundant tree species in the overstory and the most abundant conifer in the understory. Western redcedar (*Thuja plicata*), white fir (*Abies concolor*), and ponderosa pine (*Pinus ponderosa*) are the major overstory associates in approximate order of abundance. The understory is composed of a variety of broadleaf trees and shrubs including California black oak (*Quercus kelloggii*), Pacific madrone (*Arbutus menziesii*), poison oak (*Rhus diversiloba*), oceanspray (*Holodiscus discolor*), and red-flowering currant (*Ribes sanguineum*). Bigleaf maple (*Acer macrophyllum*) and Pacific yew (*Taxus brevifolia*) occur in moist areas.

Methods

We set 80 Sherman live traps (9 cm by 7.5 cm by 23.5 cm) in four parallel lines of 20 traps each, with intertrap intervals of 20 m. Interline distances were 20 m, 60 m, and 20 m. A small wad of cotton was placed in each trap, and the trap was covered with an aluminum shelter to mitigate the influences of temperature and moisture on the survival of captured animals. Each trap was baited with rolled oats. Traps were opened during nine trapping sessions between 1981 November and 1982 November for a total of 1840 trap nights (Table 1). No trapping was done in 1981 December, or in 1982 January,

March, and October. Whenever possible, fecal pellets were collected from captured adult *Clethrionomys* with forceps as they were expelled from the anus and immediately placed in 2-percent formalin. A total of 163 samples was collected during the study.

Fecal samples were oven-dried for 24 h at 80°C and then weighed to the nearest 0.001 g. Each dried sample was macerated in 0.5 ml Tween solution (J. T. Baker Chemical Co., Phillipsberg, New Jersey). A drop of Melzer's reagent (Stevens 1974) was added to two to three drops of the Tween-pellet solution. One drop of this mixture was placed on the counting chamber of a hemocytometer and covered with a 22 mm², No. 1 glass cover slip.

Individual fungal spores present in each of the 320 squares comprising the central mm² of the hemocytometer grid were identified to genus. The total number of occupied squares per genus was recorded. The entire chamber was then scanned for less frequently occurring genera. Identification techniques are described by McIntire (1984).

Because differences in spore numbers could be a function of pellet size, the total number of squares per genus was divided by dry weight to obtain an index of spore abundance (SAI) for each genus in each fecal sample. Genera of fungal spores identified in the fecal sample, but absent in the counting area, were used in calculations of mycotrophic diversity, percent frequency of occurrence, and average number of genera per sample.

Relative abundance of each genus was calculated by dividing the sum of SAI values for a genus by the sum of SAI values for all genera in a given sampling period. Percent frequency of occurrence was calculated for each genus by dividing its frequency by the number of samples collected during that sampling period. Fungal diversity in the diet was calculated for each sample period using Shannon's (1948) diversity index:

$$H' = - \sum_{i=1}^N p_i \ln p_i$$

where p_i is the proportion of SAI values contributed by genus i and N is the number of genera identified in the sampling period. For diversity indices, genera present in the sample

TABLE 1. Percent frequency of occurrence of fungal genera in fecal pellets for each sample period.

Fungal genus	1981 ¹				1982 ¹					Mean
	NOV 22-24	FEB 19-20	APR 8, 22-23	MAY 12-13, 20	JUNE 15-16, 22	JULY 28-30	AUG 22-23	SEP 25-26	NOV 22-23	
<i>Rhizopogon</i>	87.5	33.3	28.6	45.0	100.0	93.9	66.7	81.2	85.7	69.0
<i>Gautieria</i>	18.8	26.7	21.4	40.0	11.1	46.7	47.6	56.2	35.7	33.8
<i>Hysterangium</i>	6.2	6.7	3.6	20.0	16.7	6.7	33.3	56.2	35.7	20.6
<i>Leucogaster</i>	18.8	6.7	7.1	15.0	--	26.7	42.9	31.2	7.1	17.3
<i>Melanogaster</i>	--	--	--	5.0	5.6	40.0	23.8	37.5	--	12.4
<i>Calvatia</i>	--	--	17.9	30.0	16.7	6.7	23.8	12.5	--	12.0
<i>Hymenogaster</i>	--	13.3	25.0	15.0	11.1	--	--	--	--	7.2
<i>Hydnotrya</i>	6.2	--	--	--	27.8	6.7	4.8	12.5	7.1	7.2
<i>Martellia</i>	--	--	--	--	--	20.0	19.0	18.8	--	6.4
<i>Tuber</i>	6.2	--	--	--	--	--	9.5	18.8	7.1	4.6
<i>Octavianina</i>	--	--	--	--	--	6.7	14.3	12.5	--	3.7
<i>Microthecium</i>	--	--	--	--	--	--	4.8	--	28.6	3.7
<i>Geopora</i>	18.8	--	--	--	--	--	--	--	14.3	3.7
<i>Genea</i>	--	--	--	5.0	--	--	--	--	14.3	2.1
<i>Elaphomyces</i>	--	--	3.6	--	--	6.7	--	6.2	--	1.8
<i>Endogone</i>	--	--	--	--	--	--	--	--	7.1	.8
<i>Gastroboletus</i>	--	--	--	--	--	--	--	--	7.1	.8
<i>Genabea</i>	--	--	--	--	5.6	--	--	--	--	.6
<i>Glomus</i>	--	--	--	5.0	--	--	--	--	--	.6
Number of genera	7	5	7	9	8	10	11	11	11	
Number of samples	16	15	28	20	18	15	21	16	14	

¹No sampling was conducted during 1981 December, or 1982 January, March, October.

but absent in the counting area were arbitrarily assigned a value of 1 for each sample in which the genus occurred.

Temporal variation between sample periods in SAI values per sample was tested for statistical significance by the nonparametric Kruskal-Wallis test, and temporal variation in the number of fungal genera per sample was tested by analysis of variance. Arcsin transformation of the relative abundance data was performed to meet the assumption of a normal distribution (Snedecor and Cochran 1980), and analysis of variance with the transformed values was performed to test statistical significance of temporal variation.

Results

Spores of 19 fungal genera were identified in the *Clethrionomys* fecal pellets (Table 1). Spores identified as *Rhizopogon* and *Martellia* may include related genera that are morphologically indistinguishable. All but two of the identified genera are probably hypogeous mycobionts.

Calvatia is always epigeous, and *Microthecium* is parasitic on *Geopora*.

Rhizopogon, the most frequently occurring genus, was present in at least 25 percent of the samples in all sample periods (Table 1). *Gautieria*, the second most frequently occurring genus, was found in over 25 percent of the fecal samples in two-thirds of the sampling periods. *Gautieria* and *Hysterangium* were present in the diet throughout the year. The only other genus with nearly year-round presence, *Leucogaster*, was absent in the June sample. *Hymenogaster* occurred from late fall through early summer but was most frequently found in the fecal samples collected in the spring. *Calvatia*, *Hydnotrya*, and *Melanogaster* exhibited bimodal frequency distributions, with one peak in early to late summer and one peak in the fall. *Tuber*, *Martellia*, and *Octavianina* were primarily present in the fecal samples during the late summer and fall. The remaining genera occurred in the fecal samples infrequently or sporadically.

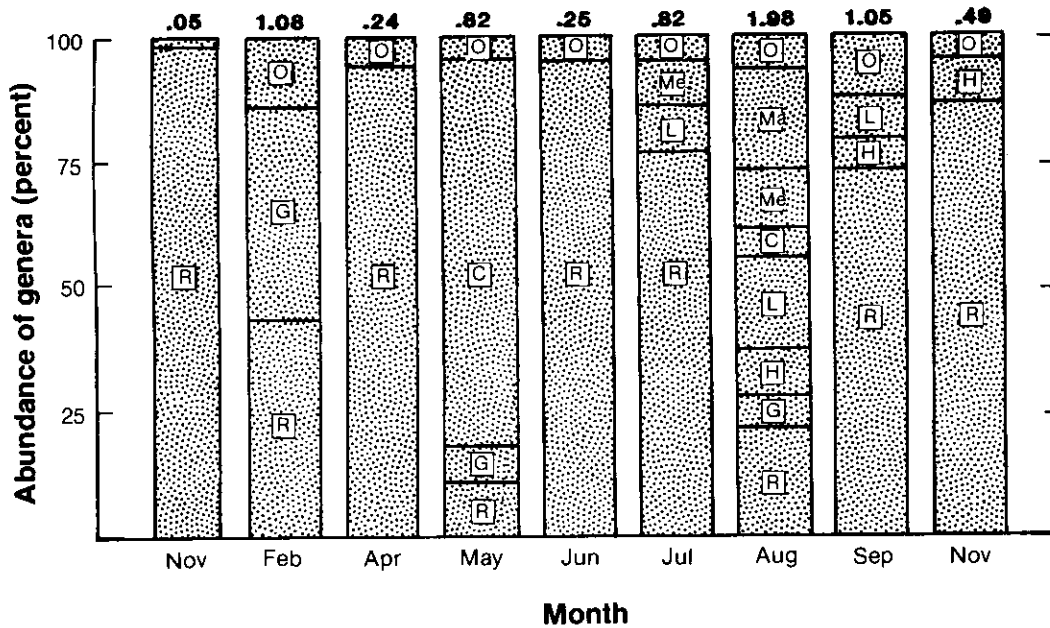


Figure 1. Relative abundance of genera and fungal diversity indices by sampling period. Genera contributing <5 percent are combined as "other." Fungal diversity indices are presented at the top of each bar. C = *Calvatia*; G = *Gautieria*; H = *Hysterangium*; L = *Leucogaster*, Ma = *Martellia*, Me = *Melanogaster*, O = other, and R = *Rhizopogon*.

The relative abundance of different fungal genera varied significantly by sample period ($F = 16.65$; $df = 16, 136$; $P < 0.01$) (Fig. 1). *Rhizopogon* was the most abundant genus of mycorrhizal fungi in all sample periods and was the most abundant genus of all types of fungi in all sample periods, except May when *Calvatia* spores were more abundant.

Rhizopogon contributed at least 10 percent of the total spores in every sample period, whereas no other genus contributed >10 percent in more than one sample period. The disproportionately high SAI value for *Rhizopogon* in the November 1981 sample period in conjunction with low SAI values for other genera resulted in an extremely low diversity index (0.05). In August 1982, eight genera contributed at least 5 percent of the total number of spores, resulting in the highest diversity index value (1.98). No other sample period had more than three genera with each contributing more than 5 percent of the total number of spores.

The mean number of genera per sample ex-

hibited statistically significant temporal variation ($F = 7.34$; $df = 8, 154$; $P < 0.01$). The highest mean value (3.44) occurred in the September samples, and the lowest mean value (1.07) occurred in the February samples (Fig. 2).

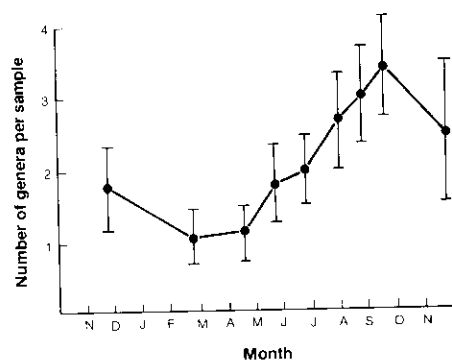


Figure 2. Mean number of genera per sample in fecal samples collected from red-backed voles trapped from 1981 November to 1982 November. Vertical bars represent 95 percent confidence intervals.

The SAI value of all genera combined per sample varied significantly by sample period ($H = 56.92$, $df = 8$, $P < 0.005$). The lowest mean value occurred in February, and highest value occurred in July (Fig. 3). The 1981 November and 1982 November samples had similar mean SAI values.

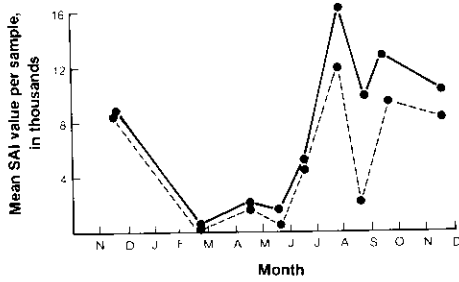


Figure 3. Mean SAI values per sample for all genera combined (solid line) and *Rhizopogon* (broken line) for fecal samples collected from red-backed voles trapped from 1981 November through 1982 November. SAI = spore abundance index.

The patterns of mean SAI values for *Rhizopogon* and the mean SAI values for all genera combined were similar for all sample periods except August when *Rhizopogon* SAI values decreased dramatically (Fig. 3). High mean SAI values for *Gautieria*, *Leucogaster*, *Martellia*, *Hysterangium*, and *Melanogaster* in the August sample accounted for this difference (Fig. 4). The mean SAI value of *Melanogaster* was relatively low in the September sample despite a high frequency of occurrence. *Calvatia*, the only genus of epigeous fungi present in the samples, exhibited a different pattern of mean SAI values than any of the hypogeous fungal genera. The mean SAI value for *Calvatia* was highest in May, when mean SAI values for hypogeous fungal genera were low. Except for mean SAI values for *Octavianina*, which were 390 for both August and September samples, mean SAI values for all other genera were less than 150 for all sample periods.

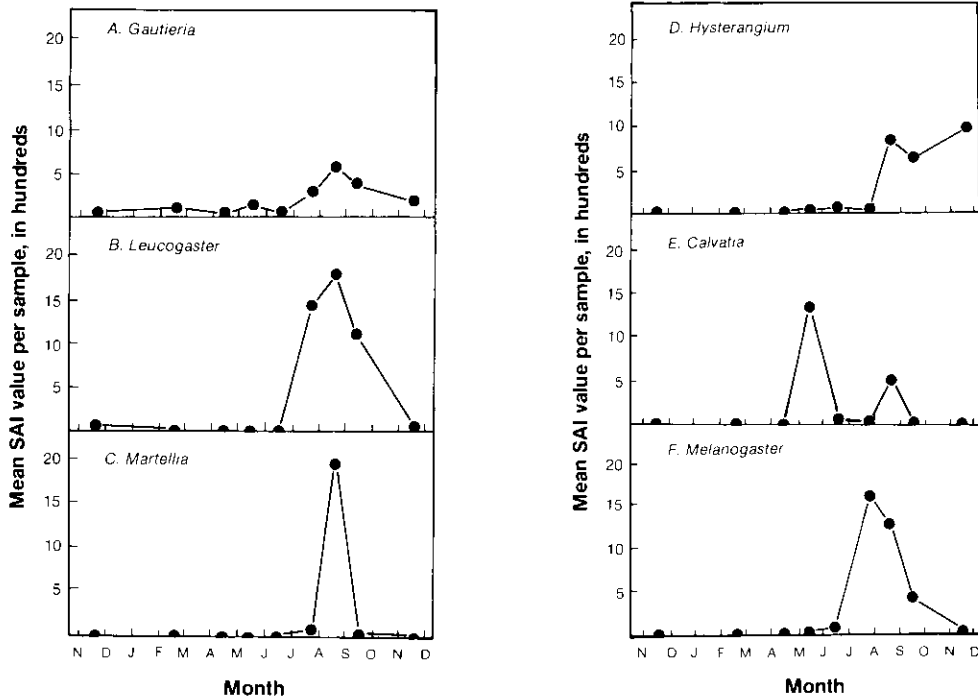


Figure 4. Mean SAI value per sample of six genera in fecal samples collected from red-backed voles trapped from 1981 November through 1982 November.

Discussion

Fogel (1976), working in the Oregon Coast Range, presents the only published data on hypogeous sporocarp abundance and phenology. Although species exhibited variation in fruiting phenology, the total mycorrhizal sporocarp population exhibited a bimodal productivity curve, with a spring peak in April to May and a fall peak in October to December. Spring sporocarp abundance increased logarithmically as the mean minimum air temperature increased from 0°C to 6°C. The decrease in number of sporocarps in the summer was attributed to a decrease in soil and litter moisture. Production of sporocarps in the fall increased with the onset of autumn rains until mean minimum air temperatures decreased to 4°C. Although Fogel noted that mycophagy may have influenced his estimate of production of sporocarps, he did not examine the relationship between mycophagy and sporocarp abundance.

The climate of our study area differs from that of Fogel's Coast Range site. Although no meteorological data were collected at our study site, data from Hyatt Reservoir, the closest active weather station (located 20 km south of the study area, T39S, R3E, Section 16, elevation 1500 m), can be used as an indication of meteorological trends for the general area. From 1981 November through 1982 May and in 1982 November the mean minimum air temperatures were below 0°C at Hyatt Reservoir (unpublished data, U.S. Weather Bureau, Medford, Oregon). These temperatures contrast with those during Fogel's three-year study, where subzero mean monthly minimum temperatures occurred only three times: 1972 December, 1973 January, and 1974 January. With the onset of autumn and winter precipitation at Hyatt Reservoir, mean minimum temperatures dropped below 0°C. Assuming similar meteorological trends at our study site, and that microclimatic effects on production of sporocarps are stimuli similar to those in the Coast Range, the primary fruiting seasons at our study site are relatively short. Low temperatures between the late fall and spring probably restrict sporocarp production, resulting in a unimodal sporocarp productivity curve with primary production in summer and fall.

The close association between observed SAI values and meteorological trends at Hyatt Reser-

voir corresponds with Fogel's observations concerning the influence of weather on sporocarp production. Spore abundance was lowest in the February through May samples, when monthly mean minimum air temperatures were below 0°C at Hyatt Reservoir. With a rise in the mean minimum air temperature above 0°C, the total number of spores increased dramatically in the June and July samples and remained relatively high through the November sample. This association suggests that in southwestern Oregon, *Clethrionomys* may consume hypogeous sporocarps in relation to their availability.

High SAI values occurred in both 1981 November and 1982 November samples despite mean minimum air temperatures below 0°C at Hyatt Reservoir during those periods. The higher-than-expected SAI values may have resulted from a delay between the cessation of sporocarp production and the time most of the sporocarps were consumed, as suggested by Ure and Maser (1982). An alternative explanation is that mean minimum air temperatures dropped below 0°C at our study site at a later date, extending optimal sporocarp production through November.

Although *Clethrionomys californicus* are fungus and lichen specialists (Ure and Maser 1982), we hypothesize that they are generalists in selection of available sporocarps. *Rhizopogon*, the predominant genus of fungi in the fecal samples, is also by far the most abundant genus of hypogeous fungus in coniferous forests of southwestern Oregon, fruiting most abundantly in the late summer and autumn months (J. M. Trappe, personal communication). In late summer and autumn, the diversity and abundance of other genera of hypogeous fungi increase dramatically. This pattern of sporocarp abundance is the same trend we observed for SAI values of different fungal genera.

These trends are similar to those exhibited by western red-backed voles in other areas in the Oregon Cascade Range (Ure and Maser 1982). In the Coast Range, however Ure and Maser (1982) found a different pattern of fungus consumption, with no apparent correlation between hypogeous sporocarp availability and the degree of mycophagy by western red-backed voles. They attributed the different pattern to an abundance of sporocarps that exceeded forage demand

during certain times of the year, and voles feeding on cached sporocarps when availability was low. In the Cascade Range, the shorter season for sporocarp production and corresponding paucity of sporocarps during certain seasons probably account for the closer relationship between sporocarp abundance and mycophagy by western red-backed voles.

In a study by Ure (personal communication), *Rhizopogon*, *Gautieria*, *Hysterangium*, and *Leucogaster* were the most frequently occurring genera, in descending order of frequency, in the stomachs of western red-backed voles from the Cascade Range. These genera also occurred most frequently in our study, in the same order of frequency. This contrasts to Ure's findings for the diet of Coast Range animals, which fed primarily on *Rhizopogon*, Hydnangiaceae, Endogonaceae, and *Gautieria*. *Rhizopogon* has also been identified as the major fungal constituent in the diet of other small mammals, including Siskiyou chipmunks (*Tamias siskiyou*) in southwestern Oregon (McIntire 1984), northern flying squirrels (*Glaucomys sabrinus*) in northern Oregon (Maser *et al.* 1985), and western gray squirrels (*Sciurus griseus*) in various locations in California (Stienecker and Browning 1970, Stienecker 1977).

McIntire (1984) hypothesized that hypogeous sporocarp distribution influences the distributions of some small mammal species. Similarly, western red-backed voles may select microhabitats that optimize opportunity for foraging on hypogeous sporocarps during months when sporocarps are abundant and select microhabitats that optimize utilization of other food resources, such as lichens, during other seasons. This phenomenon would be moderated or absent in areas in which sporocarps are more consistently available, such as the Coast Range.

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Literature Cited

- Fogel, R. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. *Can. J. Bot.* 54:1152-1162.
- Franklin, J. F., K. Cromack, Jr., W. Denison, *et al.* 1981. Ecological characteristics of old-growth Douglas-fir forests. USDA For. Serv. Gen. Tech. Rep. PNW-118. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon.
- Franklin, J. F., and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8. Pac. Northw. For. and Range Exp. Sta., Portland, Oregon.
- Gashwiler, J. S. 1959. Small mammal study in west-central Oregon. *J. Mammal.* 40:128-129.
- _____. 1970. Plant and mammal changes on a clearcut in west-central Oregon. *Ecology*, 51:1018-1026.
- _____. 1977. Reproduction of the California red-backed vole in western Oregon. *Northw. Sci.* 51:56-59.
- Hayes, J. P. 1983. Forestry related aspects of the ecology of *Clethrionomys californicus*. Southern Oregon State College. M.S. thesis.
- Hooven, E. F., and H. C. Black. 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. *Northw. Sci.* 50:189-208.
- Maser, C., and R. M. Storm. 1970. A key to the Microtinae of the Pacific Northwest (Oregon, Washington, Idaho). Oregon State University Bookstore, Inc., Corvallis.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978a. Fungal—small mammal inter-relationships with emphasis on Oregon coniferous forests. *Ecology* 59:799-809.
- Maser, C., J. M. Trappe, and D. C. Ure. 1978b. Implications of small mammal mycophagy to the management of western coniferous forests. *Trans. 43rd N. Amer. Wildl. Conf.*:75-88.
- Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. *Can. J. Zool.* 63:1084-1088.
- McIntire, P. W. 1984. Fungus consumption by the Siskiyou chipmunk within a variously treated forest. *Ecology* 65:137-146.
- Shannon, C. E. 1948. A mathematical theory of communication. *Bell Systems Tech. J.* 27:379-423, 623-656.

- Snedecor, G. W., and W. G. Cochran. 1980. Statistical methods. Iowa State University Press, Ames.
- Stienecker, W. E. 1977. Supplemental data on the food habits of the western grey squirrel. Calif. Fish Game 63:11-21.
- Stienecker, W. E., and B. M. Browning. 1970. Food habits of the western grey squirrel. Calif. Fish Game 56:36-48.
- Stevens, R. B., editor. 1974. Mycology guidebook. University of Washington Press, Seattle.
- Tevis, L. L., Jr. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the Sierra Nevada. J. Mammal. 33:198-205.
- _____. 1956. Responses of small mammal populations to logging of Douglas-fir. J. Mammal. 37:189-196.
- Trappe, J. M., and R. D. Fogel. 1977. Ecosystematic functions of mycorrhizae. In J. Marshall (ed.) The below ground ecosystem: a synthesis of plant-associated processes. Range Sci. Dep. Ser. No. 26, Colo. State Univ., Fort Collins. Pp. 205-214.
- 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, USDA For. Serv. Pp. 165-171.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Can. J. Zool. 60:3307-3315.

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