

FUNGAL–SMALL MAMMAL INTERRELATIONSHIPS WITH EMPHASIS ON OREGON CONIFEROUS FORESTS^{1,2}

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Abstract. Most higher plants have evolved with an obligatory symbiotic relationship with mycorrhizal fungi. Epigeous mycorrhiza formers have their spores dispersed by air currents, but hypogeous mycorrhizal fungi are dependent upon small mammals as primary vectors of spore dissemination. Mammalian mycophagists defecate within the coniferous forest ecosystem, spreading the viable spores necessary for survival and health of the conifers. As one unravels and begins to understand the interrelationships between small-mammal mycophagists and mycorrhizal fungi, it becomes apparent that the various roles of small mammals in the coniferous forest ecosystem need to be reevaluated. One can no longer accept such simplistic solutions to timber management as poisoning forest rodents to "enhance" tree survival. One must consider the direct as well as the indirect costs and benefits of timber management decisions if one is to maintain balanced, healthy coniferous forests.

Key words: *Ectomycorrhizae; higher plants; hypogeous fungi; obligatory symbiotic relationships; Oregon; rodent diet; small-mammal mycophagy; spore dispersal; vesicular-arbuscular mycorrhizae.*

INTRODUCTION

Most higher plants have evolved with a compelling dependence on symbiotic, root-inhabiting (mycorrhizal) fungi for absorption of adequate nutrients from soil (Marks and Kozlowski 1973, Sanders et al. 1975). Generally, neither mycorrhizal fungi nor their hosts can complete their life cycles independently. In this paper, we explore the significance of these interrelationships in functioning and management of ecosystems.

The common use of fungi as food by small mammals is well documented (Fogel and Trappe 1978). Most purposefully eaten fungi are higher Basidiomycetes, Ascomycetes, and Phycomycetes (Endogonaceae), and lichens. Except for lichens, only sporocarps are eaten. The sporocarps may range from 0.5–200 milli-

metres in diameter, be dull or brightly colored, and, by maturity, emit species-characteristic odors. The spores pass through the digestive tract and are excreted without morphological change or loss of viability (Trappe and Maser 1976). The other tissues are digested. Most ingested fungi can be identified to genus from spore characters alone (Fig. 1); many, including all the Endogonaceae, can be identified to species (Figs. 2, 3). Determination of ingested fungi to genus permits inferences on: (1) whether they are mycorrhizal or saprophytic; (2) if mycorrhizal, which plant or plant group was the host; and (3) whether the fungi were epigeous or hypogeous, i.e., producing their sporocarps aboveground vs. belowground and with spores disseminated primarily by moving air vs. other means.

METHODS

Mammals used in our studies were dead-trapped or shot. Standard specimen data were recorded. Stomach contents and the terminal-most fecal pellets in the colon were preserved separately in vials in 10% Formalin. For fungal analysis, each vial was shaken vigorously and opened. Narrow forceps were plunged to the bottom, closed and withdrawn. The captured material was placed on a microscope slide, a drop of Melzer's reagent (I, KI, and chloral hydrate) added and mixed, a cover slip put in place, and the slide examined microscopically. All fungal taxa were recorded with es-

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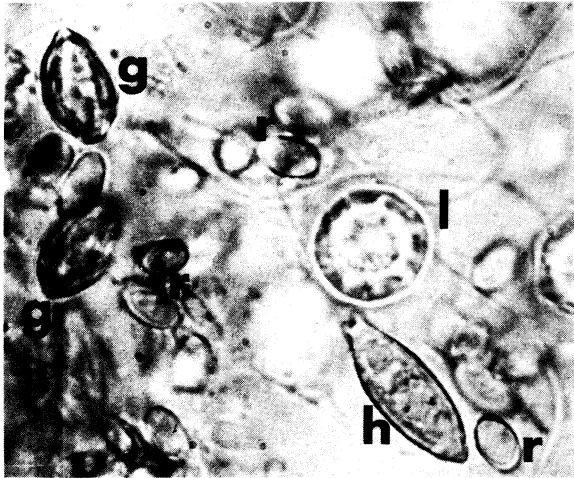


FIG. 1. Spores of hypogeous Basidiomycetes from the stomach of a northern flying squirrel, *Glaucomys sabrinus*, $\times 1,000$. G = *Gautieria* sp., H = *Hysterangium* sp., L = *Leucogaster* sp., R = *Rhizopogon* sp.

timates of the percentage by volume represented by each. Fecal pellets were sampled only to determine if additional fungal taxa had been consumed in earlier feeding by the animal.

Each fungal taxon was assumed to represent a single sporocarp. Thus, frequency of each taxon or any grouping of taxa was calculated as percentage of all sporocarps encountered in the study—the "fungal taxa frequency." The percentage of animals of a taxon containing purposefully eaten fungi, the "mycophagy frequency", was also calculated.

RESULTS AND DISCUSSION

The fungi consumed

Taxonomic groups.—Over 1000 fungal sporocarps found in the digestive tracts of >400 animals were identified (Table 1). Basidiomycetes accounted for 61% of them (Table 2).

Fruiting habit.—The preponderance (88%) of hypogeous fungi (Table 2) confirms earlier reports in which fungi in stomachs have been adequately identified (Drozdź 1966, Stienecker and Browning 1970). Most reports of drying and storage of fungi by small mammals, on the other hand, suggest that epigeous species predominate (Fogel and Trappe 1978), and our field observations might lead to similar conclusions. This seeming paradox between what is predominantly eaten and what is predominantly dried and cached can be explained by differences in structure and maturation processes of the 2 fungal groups.

Hypogeous fungi typically contain a gleba of spore-bearing tissue enclosed by a peridium (Fig. 4). When the gleba is mature, its tissues autolyse to form a slimy spore suspension surrounded by a collapsing peridium. Epigeous fungi, in contrast, expose their fertile tissue (Fig. 5) and forcibly discharge spores into the

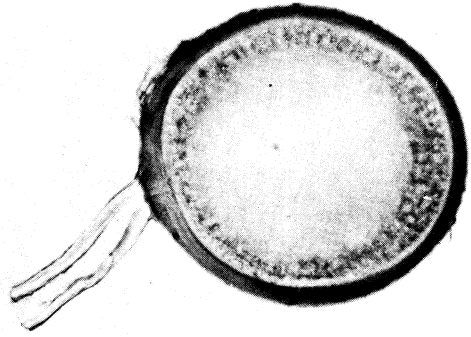


FIG. 2. Spore of *Glomus fasciculatus* (Endogonaceae) from the stomach of a sage vole, *Lagurus curtatus*, $\times 400$.

air. Fleshy species produce short-lived mushrooms that take up water rapidly during expansion. The same structures that permit rapid water uptake may also permit rapid water loss. Thus, the drying of fungi for caching is more likely to succeed for epigeous species than for hypogeous species, and caching behavior seems accommodated to the difference. Hypogeous fungi are dried and cached (Hardy 1949), but conditions for rapid drying must prevail.

The preponderance of hypogeous species in the small-mammal diet cannot be explained by relative abundance. Epigeous fungi fruit prolifically and their seasonal biomass frequently far exceeds the consuming capacity of small mammals.

Hypogeous Basidiomycetes and Ascomycetes have evolved a dependence on animals for spore dispersal. Most, if not all, appear to be obligate ectomycorrhizal



FIG. 3. Spores of *Endogone incrassata* (Endogonaceae) from the stomach of a northern red-backed vole, *Clethrionomys rutilus*, $\times 400$.

TABLE 1. Fungal taxa frequency¹ in rodent digestive tracts

Fungal taxa	Fruiting habit ²	Nutritional habit ³	Geomyidae (%)	Sciuridae (%)	Cricetidae (%)	Microtidae (%)	Zapodidae (%)	All rodents (%)
Basidiomycetes								
<i>Rhizopogon</i> and relatives ⁴	HY	EC	5	28	22	18	0	22
Hydnangiales	HY	EC	0	8	4	11	0	9
<i>Hysterangium</i>	HY	EC	0	7	0	6	0	6
<i>Gautieria</i>	HY	EC	0	9	4	6	0	6
<i>Leucogaster</i>	HY	EC	0	7	1	6	0	6
<i>Hymenogaster</i>	HY	EC	0	3	6	3	0	4
<i>Melanogaster</i>	HY	EC	0	5	2	2	0	3
<i>Radiigera</i>	HY	?	0	2	0	Trace	0	Trace
Boletaceae	EP	EC	0	Trace	0	0	0	Trace
Russulaceae	EP	EC	0	Trace	0	2	0	1
Cortinariaceae	EP	EC	0	0	0	1	0	Trace
Bolbitiaceae	EP	SA	0	0	0	1	0	Trace
Coprinaceae	EP	SA	0	0	0	Trace	0	Trace
Tricholomataceae	EP	?	0	0	0	Trace	0	Trace
Rhodophyllaceae	EP	?	0	0	0	Trace	0	Trace
Hydnaceae	EP	?	0	3	1	Trace	0	Trace
Undeterminable	EP	?	23	Trace	5	5	0	4
Ascomycetes								
<i>Tuber</i>	HY	EC	0	5	3	7	0	6
<i>Elaphomyces</i>	HY	EC	0	3	4	6	0	5
<i>Geopora</i>	HY	EC	5	9	1	2	0	4
<i>Hydnotrya</i>	HY	EC	0	Trace	0	2	0	1
<i>Genea</i>	HY	EC	0	3	0	1	0	2
<i>Picoa</i>	HY	EC	0	0	0	1	0	1
<i>Choiromyces</i>	HY	EC	0	Trace	2	1	0	1
<i>Balsamia</i>	HY	EC	0	Trace	0	Trace	0	Trace
<i>Barssia</i>	HY	EC	0	Trace	1	Trace	0	Trace
<i>Genabea</i>	HY	EC	0	Trace	0	0	0	Trace
<i>Fischerula</i>	HY	EC	0	0	0	Trace	0	Trace
Pyrenomycetes	EP	SA	23	0	0	4	0	2
Undeterminable	EP	?	35	2	7	1	0	1
Phycomycetes								
<i>Glomus</i>	HY	VA	9	4	25	6	75	9
<i>Sclerocystis</i>	HY	VA	0	0	6	Trace	17	1
<i>Endogone</i>	HY	EC	0	Trace	4	13	8	2
<i>Endogone</i>	EP	SA	0	Trace	1	1	0	1
Lichenes								
	AR	AL	0	1	2	4	0	3
Total			100	100	101	100	100	100

¹ Percentage of all sporocarps found; trace = <0.57%.

² HY = hypogeous, EP = epigeous, AR = arboreal (fruticose).

³ EC = ectomycorrhizal, VA = vesicular-arbuscular mycorrhizal, AL = algal symbiont, SA = saprophytic.

⁴ *Alpova* and *Truncocolumella*, spores of which cannot be differentiated from *Rhizopogon*.

symbionts with woody plants. We believe that the correlated processes of spore maturation and intensified odor emission are adaptations that extend chances for spore dispersal.

The higher proportion of hypogeous fungi in mammalian digestive tracts may partly reflect their extended seasonal availability (Fogel 1976), but it occurs also when epigeous fungi abound. This suggests the primacy of odor over sight in detection of fungi by small mammals, as already demonstrated for deer mice, *Peromyscus maniculatus* (Howard et al. 1968). Because many epigeous fungi also have strong odors, differential palatability or nutritional value may also be involved in the preference for hypogeous fungi.

Endogonaceae represent a different situation than

the hypogeous Ascomycetes and Basidiomycetes. Many species in this primitive family fruit as single spores in soil; some of these also form small sporocarps; others fruit only in sporocarps (Gerdemann and Trappe 1974). We found only sporocarp-forming species in rodent digestive tracts (Table 3). The sporocarps, usually <10 millimetres in diameter, normally comprised a small proportion of the volume in individual stomachs. Endogonaceae that fruit as individual spores in soil can be dispersed with movement of that soil (McIlveen and Cole 1976). Sporocarpic species have no spore discharge mechanism and many are presumably strongly dependent on animal mycophagy for dispersal.

The lichens detected in digestive tracts of Sciuridae,

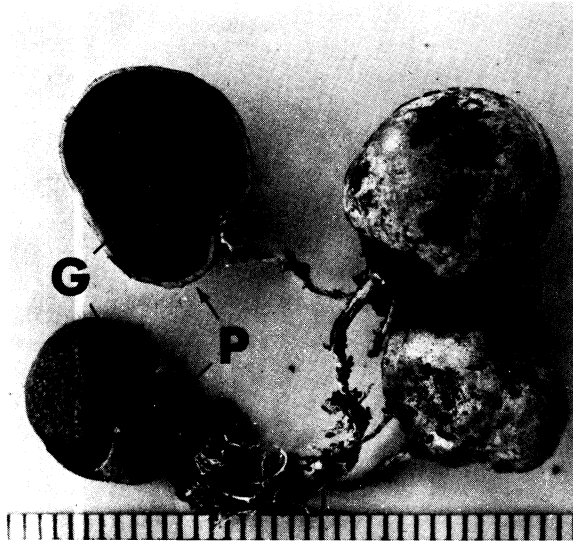


FIG. 4. Sporocarps of a hypogeous Basidiomycete, *Hysterangium separabile* (scale in millimetres). Upper left, cut in half to show gleba (G) and peridium (P) in cross section. Lower left, peridium peeled off part of surface to expose gleba. Right, surface of sporocarps.

Cricetidae, and Microtidae were all fruticose species typically epiphytic on tree stems or branches. Numerous lichen-bearing twigs fall to the forest floor during wind storms.

Nutritional habit.—Ectomycorrhizal fungi strongly predominated in the fungal diet of the small mammals studied (Table 2). This relates to the predominance of hypogeous Ascomycetes and Basidiomycetes, ectomycorrhizal fungi associated with the Pinaceae, Fagaceae, Salicaceae, Betulaceae, and a few other host plant families. Lichens and saprophytic fungi also abound in ectomycorrhizal forests but comprised only a small proportion of the fungi consumed.

The Endogonaceae include saprophytic, ectomycorrhizal, and vesicular-arbuscular (VA) endomycorrhizal species (Table 3). VA mycorrhizae are formed by Endogonaceae with most higher plants that are not ectomycorrhizal, including the Cupressaceae, Taxodiaceae, Aceraceae, and most herbaceous plants. Most plants of streambanks, meadows, prairies, early stages of forest succession, forest understories, or forests containing VA-mycorrhizal tree species have VA-mycorrhizal Endogonaceae associated with their roots.

Mammals dependent on ectomycorrhizal fungi for food will be scarce in forests of VA-mycorrhizal trees such as *Sequoia sempervirens*. "Arboreal" species that eat hypogeous fungi clearly spend time on the ground. If 1 mammal species consumes mostly fungi and another does not, the 2 do not compete for food, even though they forage in the same strata of the habitat.

Fungal diversity of the small mammal diet.—Our present data suggest preference of Endogonaceae over



FIG. 5. Sporocarp of an epigeous Basidiomycete, *Russula cascadenis*, $\times 0.5$. The gills on the underside of the cap produce spores that are forcibly discharged into the air.

other hypogeous fungi by the Pacific jumping mouse, *Zapus trinotatus* (Tables 1, 3, and 4), a behavior also reported for shrews (Whitaker and Maser 1976). Although this may be related to habitat, which contains mostly VA-mycorrhizal shrubs and forbs, 1 mouse had also consumed *Endogone lactiflua*, an ectomycorrhizal associate of conifers (Table 3). Where *E. lactiflua* occurs, usually so do hypogeous Basidiomycetes and Ascomycetes, but none had been eaten.

The data for other animals do not indicate preference for some hypogeous fungi over others. Mammals with high frequency and volume of fungi in their diet also tend to contain relatively large numbers of fungal taxa in individual digestive tracts; some individuals of the California red-backed vole, *Clethrionomys californicus*, contained 12 to 13 different fungal taxa (Table 4). The Microtidae and Sciuridae notably contained several species.

TABLE 2. Fungal taxa frequency¹ in small mammal digestive tracts by taxa, fruiting habit, and nutritional habit

Fungal group	Frequency (%)
Taxa	
Basidiomycetes	61
Ascomycetes	23
Endogonaceae	13
Lichenes	3
Total	100
Fruiting habit	
Hypogeous	88
Epigeous	9
Lichenized	3
Total	100
Nutritional habit	
Ectomycorrhizal	79
Vesicular-arbuscular-endomycorrhizal	10
Saprophytic	3
Lichenized	3
Unknown	5
Total	100

¹ Percentage of all sporocarps found.

TABLE 3. Mycophagy frequency¹ of Endogonaceae in rodent digestive tracts collected from various habitats

Endogonaceae by nutritional habit	Habitat						
	Forest			Burns with scattered trees	Ubiquitous	Edge or shrub forbs	Sagebrush prairie
	<i>Clethrionomys californicus</i>	<i>Clethrionomys californicus mazama</i>	<i>Microtus oregoni</i>	<i>Clethrionomys rutilus</i>	<i>Peromyscus maniculatus</i>	<i>Zapus trinotatus</i>	<i>Lagurus curtatus</i>
Frequency							
Saprophytes	%	%	%	%	%	%	%
<i>Endogone incrassata</i>	0	0	0	3	0	0	0
<i>Endogone pisiformis</i>	0	5	0	0	2	0	0
All saprophytes	0	5	0	3	2	0	0
Ectomycorrhizal							
<i>Endogone</i> sp.	0	0	0	0	0	0	0
<i>Endogone flammicorona</i>	3	5	0	0	1	0	0
<i>Endogone lactiflua</i>	30	0	0	3	4	8	0
All ectomycorrhizal	33	5	0	3	5	8	0
VA-mycorrhizal ²							
<i>Glomus</i> sp.	0	0	0	0	1	8	0
<i>Glomus caledonius</i>	0	0	0	0	2	0	0
<i>Glomus canadensis</i>	0	0	0	3	0	0	0
<i>Glomus fasciculatus</i>	7	2	3	6	11	31	25
<i>Glomus macrocarpus</i>	10	2	10	0	5	23	0
<i>Glomus melanosporus</i>	0	0	0	0	1	0	0
<i>Glomus microcarpus</i>	3	0	33	3	5	0	0
<i>Glomus monosporus</i>	3	0	0	0	0	8	0
<i>Glomus mosseae</i>	0	0	0	0	1	0	0
<i>Sclerocystis rubiformis</i>	7	0	0	0	11	15	0
All VA-mycorrhizal	30	4	46	12	36	50	25
All Endogonaceae combined	40	13	32	15	24	50	25
Proportion of diet by volume	2	Trace	1	2	5	10	6

¹ Based on number of animals containing each category of Endogonaceae over total number of animals examined. Percentages are not additive when individual animals contained 2 or more species in their digestive tract.

² Vesicular-arbuscular-ectomycorrhizal.

Spore dispersal by mammals.—Spore dispersal by hypogeous fungi is linked to behavior of animal mycophagists and is limited to the territory of those animals or their predators. Spores are concentrated in fecal pellets. Animals that use latrines or defecate around their nests deposit massive spore loads. When spores from feces are rain-washed into soil, they can contact susceptible host roots. The fine roots of vascular plants are also exposed and often severed by tunneling and burrowing mammals. Spore-containing feces may be excreted close by these roots. Severed roots form callose tissue from which new root tips often proliferate to provide ectomycorrhizal infection sites.

Small mammal mycophagists that confine their life to established forests do not disperse hypogeous fungi into new habitats. However, they may maintain their food source by repeated inoculation of hypogeous fun-

gi on host plant roots. Ubiquitous or edge-dwelling mammals can enhance the invasion of nonforested vegetation types of ectomycorrhizal tree species. Deer mice or chipmunks feed on hypogeous fungi in coniferous forests and deposit spore-containing feces in adjacent nonforested areas. Seeds of mycorrhizal hosts that germinate near the feces are provided with mycorrhizal inoculum.

The fungus consumers

Insectivora: Soricidae (Shrews).—The stomach of 1 *Sorex trowbridgei* (Tables 4 and 5) contained 10% Endogonaceae by volume. Whitaker and Maser (1976) studied food habits of 5 species of shrews (totaling 269 individuals) in western Oregon (marsh shrew, *Sorex bendirei*; Trowbridge shrew, *Sorex trowbridgei*; Yaquina shrew, *Sorex yaquinae*; Pacific shrew, *Sorex pacificus*; and vagrant shrew, *Sorex vagrans*). All con-

TABLE 4. Fungal taxa frequency¹ in mammalian digestive tracts

Mammal taxa	Proportions of all fungal taxa					Fungal taxa within individuals	
	Hypogeous			Epi-geous %	Lichens %	Range	\bar{x}
	Basid-iomy-cetes %	Asco-mycetes %	Endo-gona-ceae %				
Insectivora							
Soricidae							
<i>Sorex trowbridgei</i>	0	0	100	0	0	1	1.0
Lagomorpha							
Ochotonidae							
<i>Ochotona princeps</i>	86	0	0	14	0	4-6	4.7
Leporidae							
<i>Sylvilagus nuttalli</i>	0	100	0	0	0	1	1.0
Rodentia							
Sciuridae							
<i>Eutamias amoenus</i>	62	14	10	14	0	1-4	2.7
<i>Eutamias townsendi</i>	73	20	7	0	0	1-8	3.6
<i>Spermophilus lateralis</i>	42	39	1	18	0	3-8	4.2
<i>Sciurus aberti</i>	60	32	4	0	4	3-7	5.0
<i>Sciurus griseus</i>	100	Trace	0	0	0	4	4.0
<i>Tamiasciurus hudsonicus</i>	68	12	0	16	4	4-7	5.0
<i>Tamiasciurus douglasi</i>	77	15	8	0	0	2-8	4.3
<i>Glaucomys sabrinus</i>	71	26	2	1	0	1-10	5.0
Geomyidae							
<i>Thomomys townsendi</i>	0	0	0	100	0	1	1.0
<i>Thomomys talpoides</i>	0	0	0	100	0	1-3	1.8
<i>Thomomys mazama</i>	25	25	0	50	0	1-2	1.8
<i>Thomomys bulbivorus</i>	0	0	20	80	0	1-3	1.2
Cricetidae							
<i>Peromyscus crinitus</i>	0	0	25	75	0	1-3	1.5
<i>Peromyscus maniculatus</i>	35	11	40	14	0	1-5	1.5
<i>Peromyscus leucopus</i>	0	0	100	0	0	1	1.0
<i>Peromyscus truei</i>	50	0	17	33	0	3	3.0
<i>Neotoma cinerea</i>	54	11	14	7	14	2-7	4.4
Microtidae							
<i>Clethrionomys rutilus dawsoni</i>	2	9	12	70	7	1-2	1.8
<i>Clethrionomys gapperi galei</i>	70	0	24	6	0	2-6	3.4
<i>Clethrionomys gapperi idahoensis</i>	65	10	0	25	0	3-7	4.0
<i>Clethrionomys californicus californicus</i>	41	31	14	10	4	3-13	5.0
<i>Clethrionomys californicus mazama</i>	71	20	3	0	6	2-12	4.8
<i>Phenacomys intermedius</i>	100	0	0	0	0	1	1.0
<i>Microtus pennsylvanicus</i>	11	11	22	56	0	1-2	1.8
<i>Microtus longicaudus</i>	27	9	9	46	9	1-4	3.7
<i>Microtus oregoni</i>	62	22	15	1	0	1-7	3.0
<i>Lagurus curtatus</i>	0	0	100	0	0	1	1.0
Zapodidae							
<i>Zapus trinitatus</i>	0	0	100	0	0	1-3	1.9

¹ Percentage of all sporocarps found; trace = <0.5%.

sumed hypogeous Endogonaceae, ranging from 0.6 to 6.7% in volume and 4 to 10% in frequency. The short-tailed shrew, *Blarina brevicauda*, and the smokey shrew, *Sorex fumeus*, of eastern North America also feed on Endogonaceae (Hamilton 1941, Whitaker 1962, Linzey and Linzey 1973).

Lagomorpha: (1) *Ochotonidae* (pikas).—Lagomorphs are not normally regarded as mycophagists, but the pika, *Ochotona princeps*, eats both hypogeous and epigeous fungi. Three specimens secured in the

Cascade Range of Oregon had consumed fungi (Tables 4 and 5). Dowding (1955) reported Endogonaceae (*Glomus fasciculatus*) in 3 pikas collected in the southern Canadian Rocky Mountains.

(2) *Leporidae* (rabbits).—One mountain cottontail, *Sylvilagus nuttalli*, from southeastern Oregon had eaten a hypogeous Ascomycete (Tables 4 and 5), the obtaining of which had probably required digging.

Rodentia: (1) *Sciuridae* (squirrels).—Townsend chipmunks, *Eutamias townsendi*, inhabit all succes-

TABLE 5. Fungal content and mycophagy frequency¹ of mammalian digestive tracts

Mammalian taxa	No. examined	% of diet by volume in stomachs	% frequency in diet, stomach contents and feces combined
Insectivora			
Soricidae			
<i>Sorex trowbridgei</i>	2	5	50
Lagomorpha			
Ochotonidae			
<i>Ochotona princeps</i>	10	8	30
Leporidae			
<i>Sylvilagus nuttalli</i>	2	12	50
Rodentia			
Sciuridae			
<i>Eutamias amoenus</i>	11	50	82
<i>Eutamias townsendi</i>	14	77	93
<i>Spermophilus lateralis</i>	12	44	58
<i>Sciurus aberti</i>	5	98	100
<i>Sciurus griseus</i>	1	100	100
<i>Tamiasciurus hudsonicus</i>	5	77	100
<i>Tamiasciurus douglasi</i>	3	70	100
<i>Glaucomys sabrinus</i>	12	78	92
Geomyidae			
<i>Thomomys townsendi</i>	4	Trace	50
<i>Thomomys talpoides</i>	11	1	64
<i>Thomomys mazama</i>	4	3	75
<i>Thomomys bulbivorus</i>	8	22	100
Cricetidae			
<i>Peromyscus crinitus</i>	5	Trace	80
<i>Peromyscus maniculatus</i>	83	8	65
<i>Peromyscus leucopus</i>	2	... ²	50
<i>Peromyscus truei</i>	2	... ²	100
<i>Neotoma cinerea</i>	10	34	70
Microtidae			
<i>Clethrionomys rutilus dawsoni</i>	33	44	76
<i>Clethrionomys gapperi</i>	10	72	100
<i>Clethrionomys californicus</i>	81	68	100
<i>Phenacomys intermedius</i>	1	60	100
<i>Microtus pennsylvanicus</i>	9	... ²	56
<i>Microtus longicaudus</i>	4	28	75
<i>Microtus oregoni</i>	30	36	94
<i>Lagurus curtatus</i>	16	1	25
Zapodidae			
<i>Zapus trinotatus</i>	14	10	50

¹ Percentage of all individuals with fungi in digestive tracts; trace = <0.5%.

² Data available for feces only.

sional stages of western Oregon forests from the Cascade Mountains to the coast (Gashwiler 1959, 1970). The stomach contents of *E. townsendi* proved them to be avid mycophagists (Tables 4 and 5). Stomachs of 78 *E. townsendi* examined by Tevis (1952) contained 81% fungi by volume with 88% frequency. Tevis (1953) found the following seasonal use of fungi by 48 *E. townsendi*: spring—62% by volume, 86% frequency;

summer—66% by volume, 36% frequency; fall—89% by volume, 95% frequency.

The yellow pine chipmunk, *Eutamias amoenus*, inhabits coniferous forests of central and eastern Oregon. Stomach contents we examined indicated the importance of fungi in its diet (Tables 4 and 5). Tevis (1952) studied 39 *E. amoenus*. The stomachs contained 33% fungi by volume, 38% frequency. Tevis (1953) later examined another 170 *E. amoenus* and found fungi accounted for 12% of the stomach volume (20% frequency) in spring, 40% of the volume (58% frequency) in summer, and 31% of the volume (52% frequency) in fall.

Food habits of the long-eared chipmunk, *Eutamias quadrimaculatus*, were also studied by Tevis (1952, 1953). The stomachs of 126 individuals contained 70% fungi by volume, 80% frequency. Stomachs of an additional 165 *E. quadrimaculatus* later examined contained 34% fungi by volume (59% frequency) in spring, 76% by volume (89% frequency) in summer, and 88% by volume (97% frequency) in fall. In addition, Tevis (1953) examined stomach contents of 126 lodgepole chipmunks, *Eutamias speciosus*. Fungi composed 8% of the stomach contents by volume (11% frequency) in the spring, 25% by volume (42% frequency) in the summer, and 62% by volume (73% frequency) in the fall.

The mantled ground squirrel, *Spermophilus lateralis*, occurs throughout most of central and eastern Oregon in open, dry situations. Hypogeous fungi comprised nearly half of the stomach contents we examined (Tables 4 and 5). Tevis (1952) found fungi to compose 67% of the stomach contents by volume, 82% frequency, of 71 *S. lateralis*. Tevis (1953) studied the stomach contents of another 273 *S. lateralis*; fungi formed 29% of the contents by volume (53% frequency) in the spring, 65% of the volume (81% frequency) in the summer, and 90% of the volume (100% frequency) in the fall.

The red squirrel, *Tamiasciurus hudsonicus*, occupies the forest of northeastern Oregon whereas the chickaree, *Tamiasciurus douglasi*, inhabits coniferous forests throughout the rest of the state. We examined 3 stomachs from *T. douglasi* and 5 from *T. hudsonicus*; all had been feeding primarily on hypogeous fungi (Tables 4 and 5). Much of the considerable time spent by *Tamiasciurus douglasi* on the ground is presumably employed in gathering hypogeous fungi.

We examined Abert squirrels, *Sciurus aberti*, from Arizona; they had eaten hypogeous fungi almost exclusively (Tables 4 and 5). Abert squirrels primarily inhabit mature ponderosa pine forests (Patton and Green 1970) with a canopy coverage of >60% (Patton 1975). Stephenson (1975) stated that Abert squirrels eat fungi throughout the year but especially during the summer. He found that hypogeous and epigeous fungi together formed 39% by volume of the squirrels' diet from August 1972 to July 1973. Stienecker and Brown-

ing (1970) examined stomachs of the western gray squirrel, *Sciurus griseus*, in northern California with collections from every month of the year. Hypogeous fungi ranged from a low of 26% by volume (6% frequency) in May to a high of 86% by volume (17% frequency) in June. The single specimen of the western gray squirrel that we examined contained only hypogeous fungi (Tables 4 and 5).

Northern flying squirrels, *Glaucomys sabrinus*, are associated with coniferous forests in Oregon. Stomachs of 12 of these nocturnal squirrels contained mostly hypogeous fungi (Tables 4 and 5). McKeever (1960) found scant mention of fungi in the literature on food habits of *G. sabrinus*. However, his own data on stomach contents of 24 flying squirrels trapped throughout the year indicated dependence on fungi and lichens.

(2) *Geomyidae* (gophers).—The camas pocket gopher, *Thomomys bulbivorus*, originally inhabited the Willamette prairie of western Oregon, but over the years, most of the prairie has been converted to agriculture, so now *T. bulbivorus* primarily inhabits agricultural lands. We sampled *T. bulbivorus* taken in the vicinity of Corvallis, Benton County, in pastures and seed grass fields. All had eaten Endogonaceae and epigeous fungi (Tables 4 and 5).

Townsend pocket gophers, *Thomomys townsendi*, and northern pocket gophers, *Thomomys talpoides*, from eastern Oregon were examined. Both species had minor amounts of fungi in their stomachs (Tables 4 and 5). Mazama pocket gophers, *Thomomys mazama*, from grassy areas within ponderosa pine forests in central Oregon also had eaten small amounts of both hypogeous and epigeous fungi (Tables 4 and 5).

Thomomys bulbivorus and *T. townsendi* mainly inhabit grasslands and agricultural areas and so would not usually contact mycorrhizal fungi of conifers. *Thomomys talpoides*, however, is widely distributed from sagebrush communities through coniferous zones to subalpine meadows >3,000 metres elevation. Considering this wide range, a more thorough study of its food habits will probably show hypogeous fungi in its diet in some habitats.

(3) *Cricetidae* (mice).—Our largest sample was from the deer mouse, *Peromyscus maniculatus*. Fungi comprised only a trace by volume of stomach contents, but at a 62% frequency in the 21 individuals from non-forested habitats of southeastern Oregon and northwestern Nevada. The rest, from coniferous forests of western British Columbia, Canada, and western Oregon, had a total of 10% fungi by volume (73% frequency) in their stomachs. The combined total of all 83 *P. maniculatus* in our sample contained 8% fungi by volume with 65% frequency (Table 5).

Our total sample of deer mice is biased in at least 2 respects. First, most specimens were not taken during the main fungal fruiting season. Second, *P. maniculatus* is ubiquitous in distribution and opportunistic

in feeding. Sampling from a wide range of habitats on a seasonal basis is needed to fully determine the importance of fungi in its diet. Our data indicate that the fungi eaten are mostly hypogeous, including a high proportion of Endogonaceae (Tables 3 and 4).

The canyon mouse, *Peromyscus crinitus*, inhabits canyons, cliffs, and talus in the central and southeastern parts of Oregon in the Shrub-Steppe vegetational zone (Franklin and Dyrness 1973). We found a trace of fungi in 4 individuals (Table 5), but the specimens were not collected during the primary fungal fruiting season.

Two fecal samples of the pinyon mouse, *Peromyscus truei*, from mixed conifers and hardwoods of southwestern Oregon were checked; both contained fungi (Table 4). Because *P. truei* and *P. maniculatus* are sympatric in the area, comparative food habits need study to understand relationships between the 2 species and their use of the fungal flora.

We had only 2 fecal samples of the white-footed mouse, *Peromyscus leucopus*, from Iowa. One contained no fungi, the other, a trace of Endogonaceae (Table 4). Linzey and Linzey (1973) found Endogonaceae to form 1% of the volume (21.9% frequency) in stomachs from 105 *P. maniculatus* and 4.2% of the volume (30% frequency) in 40 stomachs of *P. leucopus*.

Peromyscus spp. are clearly adept at detecting Endogonaceae, apparently more so than other small mammals except for the family Zapodidae.

Although the bushy-tailed woodrat, *Neotoma cinerea*, is not usually thought of as a mycophagist, fungi are a major food in some areas (Tables 4 and 5). Most of the specimens we examined were trapped in NE Oregon where they were inhabitants of dense lodgepole pine and grand fir (*Abies grandis*) stands with little understory. The catholic nature of their diet, including fungi, allows these woodrats greater plasticity in habitat use than is generally realized.

(4) *Microtidae* (voles).—So far as we know, ours are the only available data on food habits of the California red-backed vole, *Clethrionomys californicus*. Considering the species as a whole, 68% of the contents of 81 stomachs was fungi by volume with 100% frequency (Tables 4 and 5). However, diets vary widely between subspecies.

The northern red-backed vole, *Clethrionomys rutilus*, feeds more heavily on vascular plants and fruits than on fungi, perhaps because of seasonal fungal scarcity in its far northern habitat. Thirty-three stomachs of *C. rutilus* examined from Alaska contained 44% fungi by volume (Tables 4 and 5). The boreal red-backed vole, *Clethrionomys gapperi*, also feeds extensively on fungi but has a more variable diet than *C. rutilus*. Five stomachs of *Clethrionomys g. idahoensis* from NE Oregon and 5 of *Clethrionomys g. galei* from NW Colorado all contained fungi (Tables 4 and 5).

Hamilton (1941) did not note any fungi in the stom-

achs of 100 *Clethrionomys gapperi* collected from March to December in New York. He found 75% of the stomach contents to be vascular vegetation with various amounts of fruits and insects. However, Whitaker (1962) reported Endogonaceae to have formed 20.2% of the volume in stomachs of 162 *C. gapperi* in New York. Linzey and Linzey (1973) found Endogonaceae to constitute only 0.2% of the volume of 19 stomachs of *C. gapperi* from the Great Smoky Mountains National Park on the Tennessee–North Carolina border. They stated that 64.8% of the stomach contents by volume was vascular vegetation, 12% seeds, and 4.4% insects. Williams and Finney (1964) found that Endogonaceae comprised from 5% to 100% of the volume in individual stomachs of *C. gapperi* from northwestern Wyoming and north-central Colorado. Clark (1973) found vascular plant material to form 59% of the stomach contents by volume of 25 *C. gapperi* from Grand Teton National Park, Wyoming; seed fragments 9%, hair 6%, and 26% unidentified.

One stomach of the heather vole, *Phenacomys intermedius*, was examined during the present study (Tables 4 and 5). The specimen was trapped in the Oregon Cascade Mountains along the edge of a small meadow in a small island of lodgepole pine with a *Vaccinium* spp. understory. Williams and Finney (1964) examined stomach contents of 11 *P. intermedius* from Colorado. Four contained Endogonaceae; 5 from a stream bottom had eaten no fungi; 1 from alpine tundra and 2 of 3 from 23-yr-old lodgepole pine had eaten fungi.

Stomachs of 30 Oregon voles, *Microtus oregoni*, sampled from coniferous forests of western Oregon contained 36% fungi by volume, nearly all hypogeous species (Tables 4 and 5). The long-tailed vole, *Microtus longicaudus*, is associated primarily with streams in grass/forb or brush/tree seedling successional stages and feeds on a variety of plants. However, stomachs of 4 specimens collected in coniferous forests of northeastern Oregon contained 28% fungi (Tables 4 and 5). Fecal samples of 5 out of 9 meadow voles, *Microtus pennsylvanicus*, from Iowa were found to contain fungi (Tables 4 and 5).

The sage vole, *Lagurus curtatus*, occupies sagebrush areas of the central and eastern portions of Oregon (Maser et al. 1974) as well as *Festuca ovina* communities above 2865 metres elevation in the Steens Mountains. We sampled stomachs of 16 sage voles and found *Glomus fasciculatus* (Endogonaceae) to form 1% of the stomach contents by volume with 25% frequency (Tables 4 and 5). The only other mention of fungi in the diet of *L. curtatus* is of *G. fasciculatus* in 1 individual from southeastern Alberta, Canada (Dowding 1955).

(5) *Zapodidae* (jumping mice).—The Pacific jumping mouse, *Zapus trinotatus*, is common in western Oregon in successional-stage vegetation and riparian zones. Although fruit is its main diet in summer and

fall, fungi constituted 10% by volume in stomachs of the 14 individuals that we have checked (Tables 4 and 5). Williams and Finney (1964) examined the stomach contents of 1 western jumping mouse, *Zapus princeps*, from a dense spruce-fir forest—subalpine meadow edge in Wyoming. Its stomach was full of Endogonaceae. They caught 3 more *Z. princeps* in Colorado in a meadow bordering a stream on a moraine; all contained Endogonaceae.

Linzey and Linzey (1973) examined the stomachs of 18 woodland jumping mice, *Napaeozapus insignis*, from Great Smoky Mountains National Park. They wrote: "The most interesting aspect of the food habits of *Napaeozapus* is their apparent dependence upon the fungus *Endogone* as a food. Seventy-eight percent of the animals examined contained *Endogone* spores, which amounted to almost 40% of the total food volume." Whitaker (1963) also found Endogonaceae to be a major food item in the diet of 103 *N. insignis* from Ithaca, New York. Endogonaceae formed 33.3% of the volume, 68.9% frequency, in Whitaker's specimens. *Peromyscus*, *Zapus*, and *Napaeozapus* utilize Endogonaceae to a greater degree than other small mammals studied thus far, but *Peromyscus* eats a variety of fungi, whereas *Zapus* and *Napaeozapus* select Endogonaceae.

Voles and fungi: An interpretation

An understanding of relative dependence on fungi by small mammals permits interpretation of their population changes in relation to plant succession.

Clethrionomys californicus depends on fungi for sustenance and probably also for a source of water (Getz 1968). *Microtus oregoni* feeds either primarily on fungi or primarily on vascular plants depending on habitat, but its main orientation is toward vascular plants.

The western Oregon coniferous forest can be divided into 6 generalized successional stages: (1) grass-forb; (2) brush–seedling; (3) pole-sapling; (4) young forest; (5) mature forest; and (6) old-growth forest. The dietary specialization of *C. californicus* and dietary flexibility of *M. oregoni* allow both to exist in 4 of the 6 successional stages. Their food source is partitioned in all but 1 successional stage (pole-sapling), which represents the primary change in dominance between *M. oregoni* (declining in numbers) and *C. californicus* (increasing in numbers). In this stage, hypogeous fungi become more abundant than in earlier stages while ground vegetation declines.

Some mammalian population shifts due to management stress can be understood only when differences in dependency on fungi as food is recognized. *Clethrionomys californicus* and *M. oregoni* exemplify this. In Oregon, *C. californicus* occurs only in coniferous forests and depends strongly on hypogeous, ectomycorrhizal fungi for food. *Microtus oregoni* is sympatric with *C. californicus* in these same forests. It, too,

feeds on hypogeous fungi, but its usual diet is forbs and grasses. Changes in small-mammal populations that accompany the clearcutting of old-growth coniferous timber have been studied extensively (Gashwiler 1959, 1970, 1972; Goertz 1964; Hooven 1973; and others). All studies reached the same conclusions about habitat "preferences" of *C. californicus* and *M. oregoni*: *C. californicus* is most abundant in old-growth timber and *M. oregoni* is most abundant in clearcuts, but none have explained the phenomenon satisfactorily.

Clethrionomys californicus normally disappear from clearcuts within a year after logging and burning because they are left without their specialized food supply: hypogeous mycorrhizal fungi do not fruit without their coniferous hosts. *Microtus oregoni*, however, increase in numbers as their primarily herbaceous diet becomes available.

CONCLUSIONS

Fleshy fungi are widely utilized as food by many mammals (Fogel and Trappe 1978). The study of fungal spore viability by Trappe and Maser (1976) and the present study of mammal-fungal interrelationships clearly point to the importance of mammals as spore vectors for hypogeous fungi. Further, the obligatory symbiotic relationship between mycorrhizal fungi and most higher plants—notably the commercially valuable Pinaceae—weaves a critical thread of importance to the optimum functioning of ecosystems.

"... man has defined species as economically desirable, undesirable, or neutral—good, bad, or indifferent. This may be good, short-term economics, but it is very poor ecology. We must consider both direct and indirect cost/benefits of our management decisions. No longer can we afford wildlife sacrifices on the altar of cost-effectiveness nor allow wildlife scapegoats to take the blame for interrelationships that we do not fully understand [Maser and Thomas 1978]."

In other words, we cannot validly oversimplify that certain species, such as *Peromyscus maniculatus* and *Eutamias townsendi*, impede reforestation: while they eat tree seeds, they also disperse mycorrhizal inoculum. One must objectively study and understand the role of each species as a functioning component of a dynamic ecosystem before designating it as detrimental to objectives of forest and other ecosystem management.

There is critical need for objective study of these interrelationships if we are to fulfill our obligations within the multiple-use concept of land management.

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