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# Mycophagy of red-backed voles, *Clethrionomys californicus* and *C. gapperi*

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# MYCOPHAGY OF RED-BACKED VOLES, *CLETHRIONOMYS CALIFORNICUS* AND *C. GAPPERI*

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ABSTRACT.—We examined stomach contents of 426 *Clethrionomys*, 217 *C. californicus* from western Oregon and 209 *C. gapperi* from widely scattered areas across North America. *Clethrionomys californicus* consumed fungi of 28 genera. *Clethrionomys gapperi* from the Rocky Mountains westward consumed fungi of 23 genera, whereas *C. gapperi* east of the Rocky Mountains consumed fungi of 7 genera. This study supports the conclusions of an earlier study, limited to Oregon and Washington, that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

Red-backed voles (*Clethrionomys californicus* and *C. gapperi*) in the Pacific Northwest are primary mycophagists in the coniferous forest (Hayes et al. 1986, Ure and Maser 1982); they disperse viable spores of mycorrhizal fungi (obligatory mycosymbionts of coniferous trees) and nitrogen-fixing bacteria (Li et al. 1986, Ure and Maser 1982).

Maser et al. (1978) examined stomach contents of red-backed voles and identified the mycorrhizal fungi to order. More recently, Hayes et al. (1986) also identified the mycorrhizal fungi to order but based their study on fecal analysis. Fecal analysis is biased for two reasons: fungal spores can be stored in the cecum and expelled days after a vole's last meal on a particular fungus (Maser and Maser, unpublished data), and fungal spores can be overrepresented in the feces because of differential digestion; the spores remain in good condition when many other foods have been digested.

Our purpose is twofold: (1) to compare the fungal diet of *C. californicus* from Oregon with *C. gapperi* from the West Coast to the East Coast of North America, based only on stomach analysis, and (2) to test the notion of Ure and Maser (1982) that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

## METHODS AND MATERIALS

All specimens were dead-trapped to avoid contamination of stomach contents with bait. A total of 426 *Clethrionomys* was examined over 15 years, 217 *C. californicus* from western Oregon and 209 *C. gapperi* from widely scattered areas across North America. Most specimens were quick-frozen in the field for later analysis. Stomach contents were preserved in vials of 10% formalin.

Stomach contents were microscopically examined at 100, 400, and 1,000X magnification. A small amount of material was equally mixed and randomly removed from each vial with narrow, parallel-sided forceps, placed on a microscope slide, mixed with a drop of Melzer's reagent (I, KI, and chloral hydrate), and enclosed under a 22 × 40-mm coverslip. The slide was systematically examined for fungal spores. Fungal taxa were identified with the aid of a spore key (Trappe et al., in press). The percentage by volume of fungal spores for each genus was visually estimated and recorded.

## RESULTS AND DISCUSSION

*Clethrionomys californicus* occurs from the Columbia River south through western Oregon into northwestern California. Although three subspecies are listed (Hall 1981), C. Maser has recognized only two in over 20 years of work in Oregon: *C. c. californicus* in the Coast Range and *C. c. mazama* in the Cascade Range.

*Clethrionomys californicus* has a specialized diet predominantly composed of

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TABLE 1. Percent volume of stomach contents and percent frequency, in parentheses, of fungal taxa from 217 California red-backed voles (*Clethrionomys californicus*).

| Fungal genera | *Clethrionomys californicus* | |
|---|---|---|
| | *californicus* 37[1] | *mazama* 180 |
| Basidiomycetes | | |
| *Rhizopogon* | 33.00 (70) | 31.00 (88) |
| *Alpova* | 5.00 (11) | |
| *Gautieria* | 1.20 (16) | 7.00 (58) |
| *Thaxterogaster* | | 0.20 ( 2) |
| *Hymenogaster* | 2.00 (14) | 1.00 (16) |
| *Melanogaster* | 0.40 ( 8) | 1.00 (13) |
| *Octavianina* | 1.10 ( 8) | 0.20 ( 1) |
| *Martellia* | 0.30 ( 5) | 0.40 ( 2) |
| *Radiigera* | | 0.40 ( 2) |
| *Hysterangium* | 5.00 (30) | 5.00 (46) |
| *Leucogaster* | 0.20 ( 8) | 1.00 (23) |
| *Leucophleps* | | 0.40 ( 8) |
| *Hydnangium* | | 0.01 ( 1) |
| *Hydnangiales* | 1.10 ( 8) | 1.00 (14) |
| Ascomycetes | | |
| *Cenococcum* | 0.02 ( 3) | 0.01 ( 2) |
| *Elaphomyces* | 2.40 (35) | 1.00 (15) |
| *Balsamia* | 0.02 ( 3) | 0.01 ( 1) |
| *Geopora* | 0.02 ( 3) | 0.02 ( 3) |
| *Picoa* | | 0.02 ( 3) |
| *Genabea* | | 0.01 ( 1) |
| *Genea* | 0.20 ( 5) | 0.10 ( 7) |
| *Hydnotrya* | 1.00 ( 8) | 1.00 ( 6) |
| *Barssia* | 0.30 ( 5) | |
| *Peziza* | | 0.10 ( 7) |
| *Choiromyces* | | 0.20 ( 9) |
| *Tuber* | 2.30 (30) | 0.40 ( 6) |
| Zygomyeetes | | |
| *Endogone* | 1.00 (14) | 0.10 ( 2) |
| *Glomus* | 1.00 (14) | 0.40 (12) |
| *Sclerocystis* | 0.10 ( 8) | 0.02 ( 1) |
| Epigeous | 5.00 (19) | 1.00 (10) |
| Undetermined | 12.00 (54) | 0.40 (12) |
| Lichens | 6.00 (19) | 4.00 (18) |

[1]Number of animals sampled

sporocarps of hypogeous fungi and lichens (Hayes et al. 1986, Ure and Maser 1982). *Clethrionomys c. californicus* is more strictly a mycophagist than is *C. c. mazama*. Although *C. c. californicus* eats more lichens than does *C. c. mazama* (Ure and Maser 1982) (Table 1), *C. c. mazama* eats more vascular plant material than does *C. c. californicus* (Ure and Maser 1982). As shown in Table 1, *C. c. californicus* may be more selective in the fungi it eats (seven genera with a stomach volume of 2% or more) than is *C. c. mazama* (three genera with a stomach volume of 2% or more). Both subspecies are closely associated with large, fallen trees because the wood, under closed forest canopies, remains wet throughout the year and is a site of prolonged fruiting of hypogeous fungi—the vole's specialized food (Hayes 1983, Maser and Trappe 1984, Ure and Maser 1982).

*Clethrionomys gapperi* is widely distributed across the northern United States and all but the northernmost reaches of Canada, extending south along the Rocky Mountains in the West and the Appalachians in the East. A correspondingly greater number of subspecies, 29, is recognized (Hall 1981).

The food habits of *C. gapperi* subspecies in western Washington (*C. g. nivarius* on the Olympic Peninsula and *C. g. cascadensis* in the Cascades) generally parallel those of *C. c. californicus* and *C. c. mazama*, respectively (Ure and Maser 1982) (Table 2).

*Clethrionomys gapperi* (subspecies *idahoensis* and *galei* in Table 2) consumed less hypogeous fungi in the Rocky Mountains (Merritt and Merritt 1978) than was consumed by *C. gapperi nivarius* and *cascadensis* along the West Coast (Table 2). 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. The voles are closely associated with moist habitats (Campbell and Clark 1980) that may foster and prolong fungal fruiting. Clark (1973) found that vascular plant material formed 59% of the stomach contents by volume of 25 *C. gapperi* from Grand Teton National Park, Wyoming; seed fragments 9%, hair 6%, and unidentified 26%.

Consumption of hypogeous fungal sporocarps by *C. gapperi* (subspecies *gapperi* and *carolinensis* in Table 2) decreases in percentage of volume and frequency on the East Coast. Martell (1981) studied the diet of 258 *C. gapperi* in northern Ontario. Lichens were dominant in early May and remained important throughout early summer. Fresh green plants were important from mid-May to mid-July. Seeds were important in June and early July, followed by berries in late July. Mushrooms were important in early summer and became the primary food in August and September. A similar pattern was found by Dyke (1971) in coniferous forests of the Northwest Territories and by Perrin (1979) in Manitoba. Hamilton (1941) noted no fungi in the

TABLE 2. Percent volume of stomach contents and percent frequency, in parentheses, of fungal taxa from 209 southern red-backed voles (*Clethrionomys gapperi*).

| Fungal genera | *Clethrionomys gapperi* | | | | | |
|---|---|---|---|---|---|---|
| | *nivarius* 13[1] | *cascadensis* 98 | *idahoensis* 27 | *galei* 16 | *gapperi* 25 | *carolinensis* 30 |
| Basidiomycetes | | | | | | |
| *Rhizopogon* | 13.00 (39) | 31.00 (66) | 18.00 (33) | 1.00 (38) | | |
| *Gautieria* | | 1.00 (12) | 1.00 ( 7) | 1.00 (50) | | |
| *Thaxterogaster* | 0.10 ( 8) | 1.00 (18) | 0.04 ( 7) | | | |
| *Hymenogaster* | | 0.01 ( 1) | 0.04 ( 7) | 6.00 (30) | | 0.10 (10) |
| *Melanogaster* | | 1.00 ( 3) | 0.10 ( 4) | | | 0.10 ( 7) |
| *Octavianina* | | 1.00 ( 5) | | | | |
| *Martellia* | | 1.00 ( 1) | | | | |
| *Hysterangium* | | 3.00 (18) | 0.04 ( 4) | 2.00 (19) | | |
| *Leucogaster* | 7.00 (23) | 2.00 (11) | | 0.30 ( 6) | | |
| *Leucophleps* | | | | 0.20 (30) | | |
| *Mycolevis* | | | 0.04 ( 7) | | | |
| Ascomycetes | | | | | | |
| *Elaphomyces* | | 0.04 ( 7) | | | | 1.00 (10) |
| *Balsamia* | 0.10 (31) | 0.40 ( 4) | 0.04 ( 4) | | 1.00 ( 4) | |
| *Geopora* | | 0.01 ( 2) | | 7.00 (30) | | |
| *Picoa* | 0.20 (31) | 0.01 ( 1) | | | | |
| *Genabea* | | 0.03 ( 1) | | | | |
| *Genea* | | 1.00 ( 6) | | | | |
| *Hydnotrya* | | 3.00 (22) | | | | |
| *Peziza* | | | 0.04 ( 4) | | | |
| *Tuber* | 6.00 (23) | 0.03 ( 4) | | | | 0.10 (10) |
| Zygomycetes | | | | | | |
| *Endogone* | 0.10 ( 8) | 1.00 ( 3) | | 0.10 ( 6) | | |
| *Glomus* | 1.00 (31) | 1.20 (17) | | 1.00 (19) | 40.00 (44) | 3.00 (63) |
| *Sclerocystis* | | 2.00 (12) | | | | 0.03 ( 7) |
| Epigeous | 22.00 (62) | 3.00 (13) | 15.00 (82) | 24.00 (69) | 1.00 ( 8) | 11.00 (47) |
| Undetermined | 8.00 (31) | 2.00 ( 6) | 4.00 (15) | 3.00 (30) | 0.04 ( 4) | 2.00 (10) |
| Lichens | | 20.00 (56) | 8.00 (52) | | 0.04 ( 4) | |

[1]Number of animals sampled

stomachs of 100 *C. 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. Whitaker (1962) reported Endogonaceae formed 20.2% of the volume in stomachs of 162 *C. gapperi* in New York, however. Butsch (1954) considered *C. gapperi* to be a generalist. Linzey and Linzey (1973) found Endogonaceae constituted only 0.02% 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. And Schloyer (1977) found chlamydospores, zygospores, and hyphae of *Endogone* composed 19% by volume of stomach contents from 139 *C. gapperi* in West Virginia. Invertebrates made up 1% by volume of the stomach contents. Vascular plant material was the major food and accounted for a mean of 76% of the diet by stomach volume.

*Clethrionomys californicus*, in particular, has a specialized diet predominantly composed of sporocarps of hypogeous fungi and lichens. The diet is so specialized that *C. californicus* is strictly tied to the coniferous forest habitat producing its food (Gashwiler 1970, Ure and Maser 1982).

*Clethrionomys gapperi* inhabits tremendously different habitats that include deciduous, mixed deciduous-coniferous, and coniferous forests (Gunderson 1959, Lovejoy 1975, Merritt 1981, Miller and Getz 1972, 1973, Schloyer 1977, Wharton and White 1967). In the lowlands of the Olympic Peninsula, Washington, it has a fungal diet similar to *C. californicus* (Ure and Maser 1982), but its diet becomes much more varied as its range extends northward, higher in elevation, and eastward toward the Atlantic Coast (Abbott

1961, Hamilton and Whitaker 1979, Martell 1981, Merritt 1981, Merritt and Merritt 1978, Schloyer 1977).

The West Coast forests are composed primarily of conifers with hardwoods during early succession (Franklin and Dyrness 1973, Hall et al. 1985). Eastern forests are primarily hardwoods with intermixed conifers. The western coniferous forests have a tremendous belowground biomass of hypogeous fungal sporocarps (see, for example, Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe, in press). The eastern hardwood forests lack the diversity of species, and presumably biomass, of belowground fungal sporocarps (Miller 1986), but they have a tremendous aboveground crop of mast-producing trees (Braun 1950). This study supports the conclusion by Ure and Maser (1982) that food habits of *C. californicus* and *C. gapperi* are more closely related to habitat than to species or subspecies of vole.

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