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Fungus Consumption by the Southern Red-backed Vole (Clethrionomys gapperi) in the Southern Appalachians

ABSTRACT.—We examined fungus consumption (mycophagy) by the southern red-backed vole, *Clethrionomys gapperi*, at 4 sites within two mixed mesophytic forests in the southern Appalachians in 1996 and 1999. Fecal pellet analysis was used to determine the fungi consumed by 30 voles. Overall mean spore frequency, measured as the proportion of fields of view that contained a spore, was 0.68, whereas mean frequency of plant material was 0.57 and frequency of insect material was less than 0.04. Voles primarily consumed 5 types of fungi, consisting of 4 genera and Glomalean spores, although 29 unidentified spore morphotypes were also observed. Among identified spores, mean frequency of *Melanogaster* was greatest, followed by *Coprinus*, *Elaphomyces* and Glomalean spores. Spores of *Hymenogaster* were least frequent. The consistent presence of spores in fecal pellets suggests that fungi are an important food item and that *C. gapperi* may be an important disperser of fungal spores. Compared with previous studies, our research supports the notion that *C. gapperi* is a fungal generalist and analysis of vole diets may be useful for assessing the availability of fungi for other, more specialized small mammal mycophagists such as the northern flying squirrel, *Glaucomys sabrinus*.

INTRODUCTION

Fungi are components of the diet of many small mammals (Maser *et al.*, 1978; Johnson, 1996). By consuming fungi (mycophagy), small mammals are thought to be important vectors of the propagules of many mycorrhizal fungi that exhibit a belowground (hypogeous) fruiting habit (Johnson, 1996). Our knowledge of mycophagy by small mammals stems largely from research conducted in the Pacific Northwest (*e.g.*, Maser *et al.*, 1978; North *et al.*, 1997), Australia (*e.g.*, Johnson, 1996), northern Minnesota (Pastor *et al.*, 1996; Terwilliger and Pastor, 1999) and tropical forests (Mangan and Adler, 2000). Mycophagy work in the eastern United States is restricted to a few early accounts (Hamilton, 1941; Whitaker, 1962; Fisher, 1968; Linzey and Linzey, 1973; Schloyer, 1977) and some studies examining mycophagy by *Glaucomys sabrinus* (Weigl *et al.*, 1992; S. Loeb, pers. comm.).

Clethrionomys gapperi, the red-backed vole, is an arvicoline rodent widely distributed in northern portions of North America. Along southern portions of its range *C. gapperi* is typically restricted to high-elevation areas where climatic conditions approximate boreal conditions (Merritt, 1981). In the southern Appalachians *C. gapperi* inhabits mesic habitats characterized by a northwest aspect, talus slopes and woody debris (Orrock *et al.*, 2000). The diet of *Clethrionomys* typically consists of herbaceous vegetation, although mycophagy has also been reported (Williams and Finney, 1964; Schloyer, 1977; Merritt, 1981; Maser and Maser, 1988).

We examined mycophagy by the red-backed vole in the southern Appalachians with two objectives in mind: (1) to evaluate the importance of fungi to *Clethrionomys gapperi* in the southern Appalachians and (2) to determine the potential usefulness of *C. gapperi* as an indicator of fungal availability for rare small mammal mycophagists, such as the northern flying squirrel (*Glaucomys sabrinus*), an endangered animal in the study area.

MATERIALS AND METHODS

Study area and site description.—We captured voles at 4 sites within 2 forests in the George Washington and Jefferson National Forests in Bath and Highland counties, Virginia, between 38°28′–38°02′N and 79°40′–79°50′W. Forests differed in time since last harvest: the young forest was harvested 23 y before sampling, whereas the old forest was harvested 141 y before sampling (U.S. Forest Service Continuous Inventory of Stand Condition data). Both were mixed mesophytic forests with a northwest aspect. Birch species (*Betula* spp.), sugar maple (*Acer saccharum*) and American Basswood (*Tilia americana*) were dominant canopy tree species.

Sampling methods.—Animals were sampled at the young forest on 1 May 1996 and 19 May 1999; the old forest was sampled on 26 June 1996 and 19 May 1999. Animals were sampled using pitfall traps (Type 1B of Handley and Kalko, 1993), 8 by 9 by 23 cm Sherman live traps (H. B. Sherman Traps,

Inc., Tallahassee, FL) and Museum Special snap traps (Woodstream Corp., Lititz, PA). After capture, animals were either injected with formalin or frozen until analysis.

Pooled samples were used because the technique is more efficient than using nonpooled samples and yields the same results (Colgan *et al.*, 1997). Each pooled sample consisted of fecal pellets removed from the descending colon of 2–4 randomly chosen adult animals and placed in vials with 10 drops of 10% formalin solution. Pellets were macerated within the vials and rapidly stirred. A pipette was dipped into the suspension and several drops were withdrawn. We transferred 2 drops of suspension to a microscope slide and added 1 drop of Melzer's reagent (Castellano *et al.*, 1989) and 2 drops of polyvinyl acetate (Omar *et al.*, 1979). A cover slip (22 by 22 mm) was added. For each pooled sample of 2–4 animals, 3 slides were produced.

For each slide, 25 fields of view (hereafter fields) were randomly selected for census. Spores in each field were identified to genus using the keys of Castellano *et al.* (1989). Spores in the genera *Glomus*, *Endogone*, *Gigaspora* and *Sclerocystis* (all within the Phylum Zygomycota) were classified as Glomalean fungi due to the ecological similarity of these fungi and the difficulty in correctly classifying Glomalean spores (D. L. Luoma, pers. comm.). We also noted plant material (including starch granules, pollen and vascular tissue) and insect material. Identified spores were checked against herbarium specimens and reviewed by mycologists at Oregon State University (D. Luoma and K. Jacobs), Iowa State University (R. Healy) and Virginia Polytechnic Institute and State University (S. Semones). Taxonomy of spore types follows Alexopoulos *et al.* (1996). Spores that could not be identified were classified by morphotype (L. Nicolai, pers. comm.). Frequency of occurrence was used to quantify presence of spores, plant material and insect material, and was calculated as the proportion of fields (75 per pooled sample) in which a spore was present.

Statistical analyses.—We generated a species-sample curve to determine if 75 fields were sufficient to detect most spore types. We computed means and 95% confidence intervals to compare the frequency of observed dietary items. Confidence intervals were used because they provide the same information as standard error, but also allow the ecological significance of the estimates to be interpreted and facilitate comparison with other mycophagy studies (Zar, 1996). Means are presented followed by 95% intervals (Mean; lower limit of 95% CI− upper limit of 95% CI). All analyses were performed using SPSS statistical software (Norusis, 1994).

RESULTS

A total of 975 fields was examined among 39 pooled samples representing a total of 17 adult male and 13 adult female *Clethrionomys gapperi*. Spores were detected in 666 fields (68%). Of the 2539 individual spores detected (Table 1), 2348 (92%) were identified. Thirty four unique spore morphotypes were observed, including identified and unknown spores (Fig. 1). The significant logarithmic relationship between cumulative species detected and the number of fields per slide suggests that our protocol was sufficient to detect most morphotypes with confidence (Fig. 1).

One Ascomycete genus, 3 Basidiomycete genera and Glomalean spores were identified (Table 1). Some uncertainty existed regarding whether *Melanogaster* spores were actually *Rhizopogon* (typically found in association with *Pinaceae*; D. Luoma, pers. comm.). Because pine trees were not near any of the sampling sites, these spores were classified as *Melanogaster*, whose host range includes many hardwood species (Castellano *et al.*, 1989).

Overall mean frequency of occurrence of spores in pooled fecal samples was comparable to the mean frequency of plant material occurrence, whereas insect material was rarely found (Table 1). Although our limited replication disallows statistical comparison, *Elaphomyces* was only found in the old forest and mean frequency of *Melanogaster* was greater in voles from the young forest (0.63; 0.29–0.96) compared to the old forest (0.11; 0.05–0.18).

DISCUSSION

Frequency of mycophagy by *Clethrionomys gapperi* was always >50%, and spores were usually as frequent as, or more frequent than plant material (Table 1). All spores identified in the diets of voles were of hypogeous mycorrhizal fungi, except for the epigeous saprophytic fungus *Coprinus*, suggesting that voles transport considerable numbers of mycorrhizal propagules in the southern Appalachians.

TABLE 1.—Mean frequency of occurrence and 95% confidence intervals of food items in the diets of 30 *Clethrionomys gapperi* from the southern Appalachians in 1996 and 1999. Number of individual spores of each type in parentheses. Total fungi is less than the sum of individual spore frequencies because it was not uncommon for more than 1 spore type to be found in a single field. Cells where mean frequency of occurrence was <0.01 are indicated by Trace

Food type	Mean frequency	95% Confidence intervals	
		Lower limit	Upper limit
Plant	0.57	0.36	0.78
Insect	Trace	—	—
Fungi			
Ascomycetes			
Elaphomyces	0.07 (333)	0	0.22
Basidiomycetes			
Coprinus	0.14 (525)	0.16	0.61
Hymenogaster	0.03 (31)	0	0.05
Melanogaster	0.39 (1390)	0.16	0.61
Zygomycetes			
Glomalean[a]	0.05 (69)	0.03	0.07
Unknown fungi	0.14 (191)	0.08	0.19
Total Fungi	0.68 (2539)	0.55	0.82

[a] Includes *Glomus*, *Endogone*, *Gigaspora*, and *Sclerocystis*.

Our data also suggest that voles consume different fungi in forests of differing age, although sampling during different months in 1996 and 1999 may have confounded these trends.

Although fungi were a consistent component of the diet of *Clethrionomys gapperi*, the spores we observed were often qualitatively and quantitatively different than those reported from *C. gapperi* in other regions (Table 1). Glomalean fungi may be rare (Linzey and Linzey, 1973; Schloyer, 1977; Ovaska and Herman, 1986), rare to intermediate (Williams and Finney, 1964; Schloyer, 1977; Pastor *et al.*, 1996) or dominant (Williams and Finney, 1964; Maser and Maser, 1988) in the diet of *C. gapperi*. Although they do not report the total frequency of spores in the diet of *C. gapperi*, Maser *et al.* (1978) found that 70% of the spores in stomachs of 5 voles from Colorado were Basidiomycetes, while 24% were Endogonacae and 6% were epigeous. In the same study, spores from 5 voles from Oregon were also mostly Basidiomycetes (65%), but epigeous fungi and Ascomycete fungi were more frequent (25% and 10%, respectively). Pastor *et al.* (1996) found that *Melanogaster* was in 100% of the fecal pellets examined from 33 *C. gapperi* from Minnesota, and *Hymenogaster* was in 12%. Pastor *et al.* (1996) found 16 types of fungi that did not include *Elaphomyces* or *Coprinus*, unlike our study. However, it is important to note that fecal pellet analysis may underestimate the importance of *Elaphomyces* in the diet, because small mammals typically consume the portions of the fruiting body that do not contain spores (Colgan *et al.*, 1997).

Our results support observations that *Clethrionomys gapperi* is a fungal generalist (Maser and Maser, 1988). As such, examination of *C. gapperi* diet may provide a useful representation of the fungi in an area, providing valuable data for mammalogists and mycologists alike. The usefulness of small mammals in this regard is only beginning to be appreciated, *e.g.*, small mammal diets over a 2-wk period can contain as many genera of fungi as gathered by mycologists in the same area in 3 y (Colgan, 1997). However, it should be noted that the similarity of some fungal spores (*e.g.*, *Rhizopogon* and *Melanogaster*) may also necessitate field collection of fungal sporocarps, as sporocarp morphology can be used to ascertain the correct identity of similar spore types.

Clethrionomys gapperi consumed fungal types that are prominent in the diets of northern flying squirrels (Maser *et al.*, 1986; Weigl *et al.*, 1992; Carey 1995), and may serve as an indicator of high-quality northern flying squirrel habitat. Voles are abundant in mixed mesophytic forests characterized by yellow birch (Orrock *et al.*, 2000), forests that provide important nesting habitat for northern flying

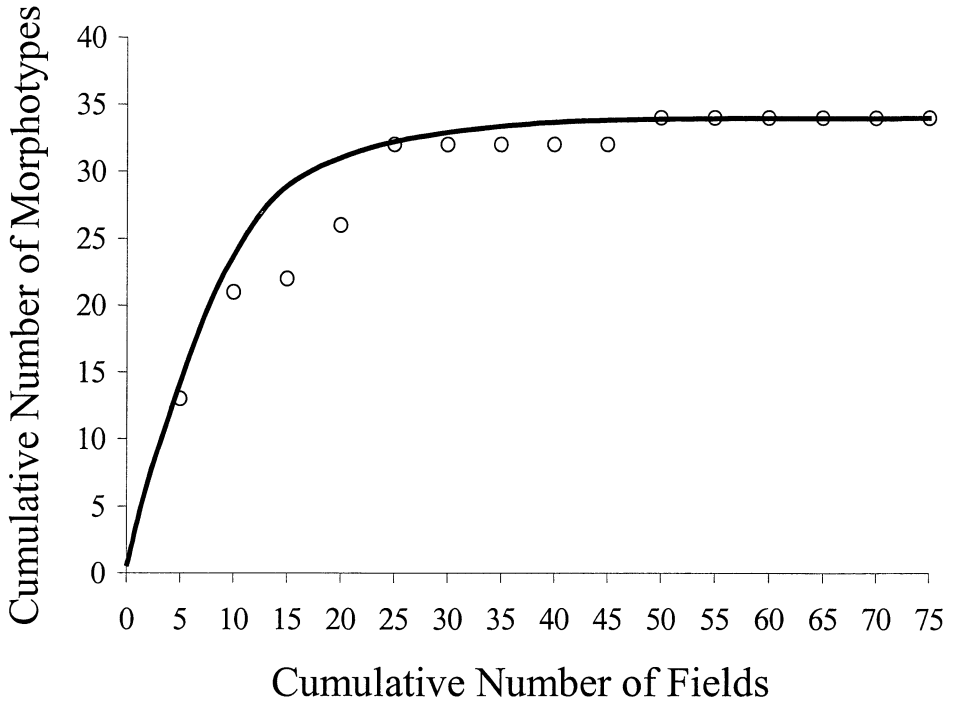

FIG. 1.—The relationship between the number of fields examined and the number of spore morphotypes observed in the diet of 30 *Clethrionomys gapperi* from the southern Appalachians in 1996 and 1999 ($R^2 = 0.99$, $F = 3601.40$, d.f. = 1,14, $P < 0.001$). Line was fitted by eye

squirrels in the region (Payne *et al.*, 1989; Weigl *et al.*, 1992). Once such habitats are located, vole fecal pellets could be collected from live traps to provide insight into the types of fungi available in the habitat, an important component of habitat quality for northern flying squirrels (Carey, 1995; Loeb *et al.*, 2000). The potential importance of voles as competitors of northern flying squirrels is also unknown and deserves examination.

Many small mammal species consume fungi (Maser *et al.*, 1978). Our results suggest that fungi are a consistent food for *Clethrionomys gapperi* and support the contention that *C. gapperi* consume different fungi across their geographic range. Vole fecal pellets can be obtained in a noninvasive fashion by live trapping, providing information about the fungi available in a habitat for voles and other small mammal mycophagists. Voles could also serve as indicators of quality northern flying squirrel habitat because of similar habitat preferences (Payne *et al.*, 1989; Weigl *et al.*, 1992; Orrock *et al.*, 2000) and because our findings suggest that voles consume fungi also consumed by *Glaucomys sabrinus*. In future studies, the importance of habitat age and treatment in affecting the types of fungi consumed deserves greater attention (North *et al.*, 1997), as our research suggests that *C. gapperi* consumed different fungi in young compared to old forests. Terwilliger and Pastor (1999) found that forest regrowth following disturbance may be related to the dissemination of fungal spores by *C. gapperi*; more research is needed to examine this possibility and its importance in the heavily managed forests of the southern Appalachians.

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