

Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada

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Abstract: The diets of a fungal specialist, northern flying squirrel (*Glaucomys sabrinus* (Shaw, 1801)), and a dietary generalist, lodgepole chipmunk (*Neotamias speciosus* (Merriam, 1890)), were examined in the old-growth, mixed-conifer forest at the Teakettle Experimental Forest in California's southern Sierra Nevada. Spores of fungi were identified from fecal pellets collected from both species during spring and summer of 1999 through 2002. Frequency of fungi in the diets of both squirrel species was consistently high across all seasons and years of study. Overall, *G. sabrinus* diets contained about 30% greater richness and evenness of fungal taxa than *N. speciosus* diets. There were no seasonal differences in richness and evenness of fungal taxa in squirrel diets. Richness of fungal taxa in diets was positively correlated with hypogeous sporocarp biomass and rainfall from June through August for *N. speciosus* but not for *G. sabrinus*. Dietary overlap between *G. sabrinus* and *N. speciosus* was high with respect to the most frequently consumed fungal taxa, although *Gautieria* and *Gastroboletus* were consumed in greater proportions by *G. sabrinus* than *N. speciosus*. Our results indicate that in the southern Sierra Nevada both *G. sabrinus* and *N. speciosus* were frequent consumers of a similar, diverse assemblage of fungal taxa and that consumption was proportional to seasonal differences in availability. For the more strongly mycophagist *G. sabrinus*, however, diet had a greater proportion of select fungal taxa and avoidance of less desirable taxa.

Résumé : Nous avons analysé le régime alimentaire d'un consommateur spécialisé de champignons, le grand polatouche (*Glaucomys sabrinus* (Shaw, 1801)) et d'un généraliste, le tamia de Californie (*Neotamias speciosus* (Merriam, 1890)) dans une forêt mixte et ancienne de conifères dans la forêt expérimentale de Teakettle dans le sud de la Sierra Nevada en Californie. Nous avons identifié les spores de champignons dans les fèces des deux espèces au cours du printemps et de l'été, de 1999 à la fin de 2002. La fréquence des champignons dans les régimes des deux espèces d'écureuils est constamment élevée durant toutes les saisons et toutes les années. Au total, le régime de *G. sabrinus* contient une richesse et une équitabilité des taxons de champignons 30 % plus grandes que le régime de *N. speciosus*. Il n'y a pas de différence saisonnière de richesse et d'équitabilité des taxons de champignons dans les régimes des écureuils. Chez *N. speciosus*, mais non chez *G. sabrinus*, la richesse des taxons de champignons est en corrélation positive avec la biomasse des sporocarpes hypogées et avec les précipitations entre juin et la fin d'août. Le chevauchement alimentaire est élevé entre *G. sabrinus* et *N. speciosus* en ce qui concerne les taxons de champignons les plus fréquemment utilisés, bien que *Gautieria* et *Gastroboletus* soient consommés en plus forte proportion par *G. sabrinus* que par *N. speciosus*. Nos résultats indiquent que, dans le sud de la Sierra Nevada, *G. sabrinus* et *N. speciosus* sont tous les deux des consommateurs fréquents d'un ensemble similaire et diversifié de taxons de champignons et que leur consommation est proportionnelle aux différences saisonnières de disponibilité de ces champignons. Cependant, chez *G. sabrinus* qui est un mycophage plus important, le régime alimentaire contient une proportion plus élevée de taxons de champignons de choix; il semble y avoir chez cette espèce un évitement des taxons moins appétissants.

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Introduction

A critical and pervasive linkage in forest ecosystems of North America is the mutualism between forest trees, mycorrhizae, and small mammals (Maser et al. 1978; Johnson 1996). Forest trees depend on mycorrhizal fungi for efficient nutrient uptake, whereas the fungi rely on their tree

hosts for carbohydrates. Mycorrhizal fungi also depend on sporocarp-consuming (mycophagous) small mammals for spore dispersal, which inoculates distant soil patches, disturbed sites, and newly formed tree roots (Pirozynski and Malloch 1988). Many forest animals are opportunistic consumers of both hypogeous (truffles) and epigeous (mushrooms) fungal sporocarps (Fogel and Trappe 1978), and

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several small mammals rely on sporocarps for a substantial portion of their diet (Maser et al. 1978). In North American forests, these include many species in the Sciuridae (squirrels, chipmunks), Geomyidae (pocket gophers), and Muridae (mice, woodrats, voles) families (Fogel and Trappe 1978; Maser et al. 1978).

Throughout the year, northern flying squirrels consume a high frequency of fungal sporocarps (Maser and Maser 1988; Waters and Zabel 1995; Currah et al. 2000) that may exceed 75% and 90% of its diet by volume (Maser et al. 1978) and frequency of occurrence (Vernes et al. 2004), respectively. In the Sierra Nevada, flying squirrels consume a high frequency and diversity of hypogeous fungal taxa but only a small percentage of non-fungal food items, including lichens and vegetation (Pyare and Longland 2001). In contrast, all chipmunks (genera *Neotamias* Howell, 1929 and *Tamias* Illiger, 1811) are dietary generalists that consume a broad spectrum of foods, including invertebrates, lichens, fungi, and seeds, leaves, flowers, and fruits of herbaceous plants and shrubs (Tevis 1952, 1953). The lodgepole chipmunk (*Neotamias speciosus* (Merriam, 1890)), a species sympatric with *Glaucomys sabrinus* (Shaw, 1801) throughout much of the Sierra Nevada, opportunistically consumes plant seeds and fruits, fungi, lichens, and invertebrates (Tevis 1953; Best et al. 1994). Recently, Pyare and Longland (2001) documented high frequency of occurrence (80%–90%) of epigeous fungi in the spring and autumn diets of both *N. speciosus* and the long-eared chipmunk (*Neotamias quadrimaculatus* (Gray, 1867)) in the Lake Tahoe Basin of the central Sierra Nevada. However, frequency and generic richness of hypogeous fungi in the diets of both species was low (30%–50%, 3 species) compared with those in the diet of *G. sabrinus* (100%, 8–15 species) in either season of their study.

The diversity and frequency of fungal taxa consumed by small mammals varies both seasonally and annually in forests of North America (Maser et al. 1985; Maser and Maser 1988; Currah et al. 2000; Lehmkuhl et al. 2004; Vernes et al. 2004). Variation in fungal consumption often is positively related to availability of fungal sporocarps (Johnson 1994; North et al. 1997; Cazares et al. 1999), but factors influencing sporocarp abundance are not well understood. In drier interior forests of western North America, sporocarp production is directly related to availability of moisture both seasonally (States and Gaud 1997) and topographically (Lehmkuhl et al. 2004). In ponderosa pine forests of northern Arizona, the biomass of hypogeous fungal sporocarps was positively associated with seasonal precipitation (States and Gaud 1997). In mixed-conifer forests of eastern Washington, where moisture declines from spring into summer and fall, biomass and richness of hypogeous sporocarps peak in the spring when moisture is still plentiful (Lehmkuhl et al. 2004). In the Sierra Nevada, where hypogeous fungal sporocarps in non-riparian mixed-conifer stands are positively associated with summer rainfall (Meyer and North 2005), fungal consumption also may increase during years of higher summer precipitation, particularly in opportunistic fungal consumers. However, such a relationship has not been previously examined for the Sierra Nevada or any other interior dry forest of North America where seasonally xeric conditions may limit fungal sporocarp production.

The purpose of our study was to examine patterns of fungal consumption by a fungal specialist (*G. sabrinus*) and a dietary generalist (*N. speciosus*) in an old-growth, mixed-conifer forest of the southern Sierra Nevada. Despite differences in dietary specialization, previous work in the southern Sierra Nevada (Izzo et al. 2005) suggested that both squirrel species consume a high diversity of similar hypogeous fungal taxa. Our goals were to determine the extent of seasonal and annual variation of hypogeous and epigeous fungal spores in the diets of *G. sabrinus* and *N. speciosus* and to examine the degree of dietary overlap in fungal taxa consumed between these two squirrel species. Additionally, we examined relationships among the abundance of fungal sporocarps, summer rainfall, and the richness of fungal taxa in squirrel diets to investigate potential mechanisms influencing seasonal and annual variability in fungus consumption.

Methods

Study area

We conducted our study at the Teakettle Experimental Forest of the southern Sierra Nevada of California. Teakettle (1800–2400 m above sea level) experiences hot, dry summers, and precipitation that falls almost exclusively in the form of snow during the winter (North et al. 2002). Mean (\pm SD) annual precipitation is 125 cm at 2100 m above sea level, and mean summer rainfall (June–August) during 1999–2002 was 1.1 ± 1.1 cm. Dominant trees include white fir (*Abies concolor* (Gord & Glend.) Lind. ex Hildebr.), red fir (*Abies magnifica* A. Murr.), sugar pine (*Pinus lambertiana* Dougl.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Teakettle is an old-growth forest characterized by a multi-layered canopy and numerous large (>100 cm diameter at breast height (DBH)) trees (many >200 years), snags, and decayed logs. In the Teakettle experiment, 18 replicate plots (4 ha each) were established and separated by buffer zones of 50–150 m. The size and spatial placement of plots were determined following variogram and cluster analysis of mapped sample quadrats (North et al. 2002).

Collection and analysis of fungal samples

Glaucomys sabrinus and *N. speciosus* were censused in all treatment plots with Tomahawk live traps (model 201; 40 cm \times 13 cm \times 13 cm). Nine sample points were established within each plot in a 3 \times 3 grid with 50 m spacing between points and a 50 m buffer from the plot boundary. Traps were attached 1.5 m high on the trunk of a large (>70 cm DBH) tree at all 9 sample points per plot. In 1999–2002, traps were placed in each plot for 3 consecutive days in early summer (June) and 4 consecutive days in mid-summer (July–August), for an annual total of 63 trap-nights per plot. In 1999–2000, all 18 plots were sampled ($n = 162$ traps and 1134 trap-nights). A random subset of plots was treated with mechanical thinning or prescribed burning in late-summer 2000–2001 for a related study (Meyer et al. 2005), so the number of untreated sampled plots was reduced to 12 ($n = 108$ traps and 756 trap-nights) and 3 plots ($n = 27$ traps and 189 trap-nights) in 2001 and 2002, respectively. We only used the untreated plots in this study to remove any potential confounding impacts of treatments on

the dietary results for *G. sabrinus* and *N. speciosus*. Traps were baited with a mixture of peanut butter and rolled oats, and a small cardboard shelter filled with polyester stuffing material was placed in each trap to provide animals with thermal insulation. Captured animals were uniquely marked with numbered ear tags, and standard measurements (mass, gender, reproductive condition) were recorded. All captured animals were handled in accordance with the American Society of Mammalogists Animal Care and Use Committee (1998) guidelines and an approved Institutional Animal and Care Use Committee (IACUC) protocol.

Fresh fecal samples were opportunistically collected from captured animals (*G. sabrinus*: 45% male and 55% female; *N. speciosus*: 42% male and 58% female; samples from juveniles of both species were excluded from the analysis). Samples were placed into individual envelopes, labeled, and stored in a dry location at room temperature for 1–6 weeks. Following the methods of Colgan et al. (1997) and Pyare and Longland (2001), small portions of all pellets in a single fecal sample (approximate total mass = 25 mg) were assessed for truffle spores. Samples were mixed with 3 mL of distilled water and a single drop was applied to each of three slides. One drop of Melzer's reagent (I, K, and chloral hydrate; Castellano et al. 1989) was added to each slide, and 25 systematically located fields of view were examined at 400× magnification (total of 75 fields of view per sample). All fungal spores present were identified to genus using a synoptic key (Castellano et al. 1989). Frequency of occurrence was calculated separately for each genus. The frequencies of two pairs of dietary genera of secotioid fungi (e.g., those producing epigeous sporocarps that remain closed; *Gymnomyces* and *Martellia*, *Cortinari* and *Thraxterogaster*) were combined, since each pair was indistinguishable based on spore characteristics alone. Fecal samples collected from individuals that were captured more than once in a particular season and year were excluded from the analysis.

Within a subset of three 4 ha plots (untreated with intensive thinning or burning), we placed a single 4 m² circular quadrat at the first eight grid points per 4 ha plot (including one quadrat at the ninth grid point in the third plot), giving a total sample area of 32 m² per plot (36 m² for the third plot), 100 m² per season (3 replicate plots; 32 + 32 + 36 m²), and 200 m² per year (100 m² × 2 seasons). In mid-June and mid-August of 2000–2002, we sampled quadrats for truffles by searching through the litter, humus, and upper 5 cm of mineral soil using a four-tined rake. We avoided sampling in the same plot location from previous years and seasons of sampling. All collected truffles were counted, placed in wax bags, dried for 24 h at 60 °C, weighed to the nearest 0.01 g, and identified to species. We used truffle collections to estimate the biomass of truffles in our study plots. All truffle voucher specimens were stored and catalogued in the USDA Forest Service Sierra Nevada Research Center Herbarium in Davis, California. Spring (June) and summer (July–August) precipitation data (1999–2002) were obtained from the Wishon Dam precipitation gauging station located 5 km from Teakettle at the same elevation.

Data analysis

We calculated frequency of fungal taxa in the diet of each squirrel species as the percentage of occurrence in the 75 fields of view per slide (one sample). Richness and evenness

(calculated with the Berger–Parker index; Magurran 1988) of fungal taxa were calculated for each species × season × year combination. We used a three-factor analysis of variance (ANOVA) to test for differences among species (*G. sabrinus*, *N. speciosus*), seasons (spring, summer), and years (1999–2002) in our dependent variables (richness and evenness of fungal taxa in diet). We conducted this analysis using data exclusively from the three plots sampled during all years of study to control for the effect of the number of sampling sites on fungal richness and evenness. We used one-factor multivariate analysis of variance (MANOVA) to examine the influence of squirrel sex on the richness and evenness of fungal taxa in squirrel diets. We used one-factor ANOVAs to examine dietary fungal richness and evenness between years of low (2001, 2002) and high (2000) hypogeous sporocarp biomass. We used one-factor ANOVAs to examine differences in dietary fungal evenness between squirrel species in each year (1999–2002). We calculated 95% confidence intervals (CI) for richness and evenness of fungal taxa in the diets of each species and for each season × year comparison. We used Pearson's product-moment correlation to examine the association between richness of fungal taxa in the diet of both squirrel species (1999–2002) with hypogeous sporocarp biomass (in June and August 2000–2003) and summer (June–August) rainfall. For these correlations, we used an α level of 0.10. Data were evaluated for normality with the Kolmogorov–Smirnov test and for homoscedasticity with Levene's test (Zar 1999). Evenness of fungal taxa, spring biomass of hypogeous fungal sporocarps, and summer rainfall data were log-transformed to meet parametric assumptions of normality and homoscedasticity. Following Vernes et al. (2001), we used a *K*-means cluster analysis to examine the degree of dietary similarity between *G. sabrinus* and *N. speciosus* for each year and season. For this analysis, we used a flexible β linkage ($\beta = -0.25$) and Sorenson's distance measurement to cluster samples defined by each squirrel species, season, and year combination. We used one-factor ANOVAs with a Bonferroni-corrected α to identify fungal taxa that were significantly different between clusters and seasons for both squirrel species in 2000 ($\alpha = 0.0023$). Additionally, we calculated Horn's index of similarity (Horn 1966) using seasonal percent occurrences of fungal taxa in the diets of the two squirrel species. This relative index ranges between 0 (no similarity) and 1 (complete similarity), with values above 0.6 expressing high dietary overlap (Krebs 1999). Analyses were conducted with STATISTICA[®] version 6.1 (StatSoft Inc. 2003).

Results

We collected 97 fecal samples from *G. sabrinus* (74 individuals) and 148 samples from *N. speciosus* (134 individuals) between 1999 and 2002. Fungal spores were present in 99% of *G. sabrinus* and 95% of *N. speciosus* fecal samples, respectively. Other consumed materials included algal cells of canopy forage lichens (*Bryoria fremontii* (Tuck.) Brodo & D. Hawksw.), fragments of vascular plant tissues, pollen of the genus *Abies*, and arthropod exoskeleton remains. A total of 21 different fungal taxa were identified in fecal samples from both squirrel species (Tables 1, 2), with 6–14 and 4–14 fungal taxa found in *G. sabrinus* and *N. speciosus* diets, re-

Table 1. Percent frequency of fungal taxa in the diet of northern flying squirrels (*Glaucomys sabrinus*) between May 1999 and September 2002.

Fungal taxon	1999		2000		2001		2002	
	Spring (N = 5)	Summer (N = 9)	Spring (N = 18)	Summer (N = 24)	Spring (N = 11)	Summer (N = 18)	Spring (N = 8)	Summer (N = 4)
<i>Elaphomyces</i>					9.1		12.5	25.0
<i>Endogone</i>								25.0
<i>Gastroboletus</i> *	40.0	44.4	72.2	29.2	63.6	50.0	37.5	
<i>Gautieria</i>	60.0	67.7	67.7	91.7	90.9	55.6	25.0	25.0
<i>Geopora</i>	20.0	33.3	22.2	33.3	9.1	16.7	50.0	
<i>Glomus</i>			5.6	4.2				
<i>Hydnotrya</i>			5.6	4.2				
<i>Hymenogaster</i>	20.0	22.2	22.2	87.5	18.2	33.3		25.0
<i>Hysterangium</i>		11.1		12.5				
<i>Leucogaster</i>		11.1		12.5		27.8		
<i>Leucophleps</i>		11.1	16.7	45.8	9.1	22.2		
<i>Melanogaster</i>	16.7	33.3	11.1	83.3	63.6	33.3		75.0
<i>Radiigera</i>		33.3	5.6	20.8	18.2	22.2		
<i>Rhizopogon</i>	100	88.9	33.3	54.2	27.3	27.8	12.5	75.0
Russulaceae [†]		22.2		8.3		5.6		
<i>Trappea</i>			5.6	20.8	27.3	11.1		
Unknown			27.8		54.6		12.5	
Total number of taxa	6	11	13 [‡]	14	11	12 [‡]	6	6

Note: Taxa with $\leq 5\%$ frequency across years and seasons are not included.

*Taxa that contain only epigeous species.

[†]Taxa that contain both hypogeous and epigeous species.

[‡]Includes one rare taxon not listed on this table.

Table 2. Percent frequency of fungal taxa in the diet of lodgepole chipmunks (*Neotamias speciosus*) between May 1999 and September 2002.

Fungal taxon	1999		2000		2001		2002	
	Spring (N = 9)	Summer (N = 24)	Spring (N = 26)	Summer (N = 17)	Spring (N = 35)	Summer (N = 8)	Spring (N = 10)	Summer (N = 19)
<i>Cortinarius/Thraxterogaster</i> *			7.7	5.9				15.8
<i>Elaphomyces</i>		12.5	7.7	11.1	34.3	25.0	20.0	15.8
<i>Endogone</i>	11.1		34.6					
<i>Gastroboletus</i> [†]	33.3	8.3	3.9		14.3			5.3
<i>Gautieria</i>	11.1	4.2	19.2		2.9			
<i>Geopora</i>	66.7	45.8	80.8	35.3	60.0	62.5		15.8
<i>Glomus</i>	22.2	16.7	7.7		8.6		30.0	5.3
<i>Hydnotrya</i>		4.2		5.9	11.4			
<i>Hymenogaster</i>	33.3	16.7	42.3	52.9	14.3	62.5		10.5
<i>Hysterangium</i>		12.5	7.7	23.5	2.9			
<i>Leucogaster</i>		12.5	3.8	5.9		37.5		
<i>Leucophleps</i>		16.7	3.8	52.9	20.0			21.1
<i>Melanogaster</i>	44.4	4.2	34.6	76.5	14.3	12.5		21.1
<i>Rhizopogon</i>	55.6	83.3	61.5	94.1	57.1	25.0	40.0	63.2
Russulaceae*		20.8		11.8	5.7			5.3
<i>Trappea</i>				23.5				5.3
Unknown		4.2	7.7				40.0	5.3
Total number of taxa	8	14	14	13 [‡]	13 [‡]	6	4	12

Note: Taxa with $\leq 5\%$ frequency across years and seasons are not included.

*Taxa that contain both hypogeous and epigeous species.

[†]Taxa that contain only epigeous species.

[‡]Includes one rare taxon not listed on this table.

spectively, from any particular season and year. Rare fungal taxa in diets included *Tuber* (5% of samples from *G. sabrinus* in spring 2000), *Pachyphloeus* (5% of samples from *G. sab-*

rinus in summer 2001), *Sclerogaster* (5% of samples from *N. speciosus* in summer 2000), and *Genabea* (3% of samples from *N. speciosus* in spring 2001).

Table 3. Results of ANOVAs for effects of season, year, and squirrel species on fungal species richness and evenness in the diets of *G. sabrinus* and *N. speciosus*.

Dependent variable	Factor	<i>F</i>	df	<i>P</i>
Fungal species richness	Season	1.071	1, 80	0.303
	Year	10.560	3, 80	<0.001
	Species	6.607	1, 80	0.012
	Season × year	0.913	3, 80	0.439
	Season × species	0.073	1, 80	0.787
	Year × species	2.387	3, 80	0.075
	Season × year × species	1.045	3, 80	0.377
Fungal evenness	Season	2.941	1, 74	0.091
	Year	7.708	3, 74	<0.001
	Species	7.489	1, 74	0.008
	Season × year	2.037	3, 74	0.116
	Season × species	0.853	1, 74	0.359
	Year × species	3.344	3, 74	0.024
	Season × year × species	0.422	3, 74	0.738

Table 4. Seasonal and annual changes in mean (\pm 95% confidence interval) richness and evenness of fungal taxa in the diets of *G. sabrinus* and *N. speciosus*.

Season and year	Richness		Evenness		Horn's index
	<i>G. sabrinus</i>	<i>N. speciosus</i>	<i>G. sabrinus</i>	<i>N. speciosus</i>	
Spring 1999	2.4 \pm 1.1	2.8 \pm 1.0	1.9 \pm 1.0	2.0 \pm 0.5	0.652*
Summer 1999	3.8 \pm 1.6	2.6 \pm 1.3	3.2 \pm 0.9	2.0 \pm 0.4	0.762*
Spring 2000	3.0 \pm 1.3	3.3 \pm 1.5	2.5 \pm 0.5	2.4 \pm 0.4	0.616*
Summer 2000	5.1 \pm 1.6	4.1 \pm 1.2	3.9 \pm 0.6	3.2 \pm 0.5	0.768*
Spring 2001	3.9 \pm 1.1	2.5 \pm 1.4	2.9 \pm 0.5	2.1 \pm 0.4	0.719*
Summer 2001	3.1 \pm 1.1	2.3 \pm 0.9	2.5 \pm 0.4	1.7 \pm 0.6	0.469
Spring 2002	2.6 \pm 1.2	1.4 \pm 1.3	1.5 \pm 0.7	1.6 \pm 0.8	0.262
Summer 2002	2.5 \pm 0.6	2.0 \pm 1.4	1.9 \pm 0.9	1.9 \pm 0.4	0.768*

Note: Dietary similarity in fungal taxa between *G. sabrinus* and *N. speciosus* was measured by Horn's index.

*Indicates high degree of dietary overlap.

Across seasons and years, mean (\pm 95% CI) richness of fungal taxa was 31% greater in *G. sabrinus* (3.5 \pm 0.3) diets than in *N. speciosus* diets (2.7 \pm 0.2; Tables 3, 4). Across seasons, richness of fungal taxa in the diet of both squirrel species was 89% and 133% greater in 2000 (4.2 \pm 0.7) than in 2001 (2.7 \pm 0.6) and 2002 (1.8 \pm 0.4; $F_{[1,88]} = 28.937$, $P < 0.001$), respectively. Across seasons in 2001, evenness of fungal taxa was 80% greater for *G. sabrinus* (2.7 \pm 0.6) than for *N. speciosus* (1.5 \pm 0.4; $F_{[1,82]} = 12.803$, $P = 0.001$), but this difference was not significant in 1999 (*G. sabrinus*: 3.0 \pm 0.9 and *N. speciosus*: 2.7 \pm 1.0; $F_{[1,82]} = 0.312$, $P = 0.578$), 2000 (*G. sabrinus*: 3.3 \pm 0.6 and *N. speciosus*: 2.5 \pm 0.6; $F_{[1,82]} = 3.577$, $P = 0.062$), or 2002 (*G. sabrinus*: 1.6 \pm 0.4 and *N. speciosus*: 1.8 \pm 0.4; $F_{[1,82]} = 0.267$, $P = 0.607$) (Tables 3, 4). Across seasons, evenness of fungal taxa in the diet of both squirrel species was 43% and 67% greater in 2000 (3.0 \pm 0.5) than in 2001 (2.1 \pm 0.3) and 2002 (1.8 \pm 0.3; $F_{[1,82]} = 19.284$, $P < 0.001$), respectively. Sex of squirrel species had no significant effect on the richness and evenness of fungal taxa in squirrel diets (*G. sabrinus*: Wilks' $\lambda = 0.977$, $F_{[2,227]} = 2.678$, $P = 0.071$; *N. speciosus*: Wilks' $\lambda = 0.992$, $F_{[2,227]} = 0.964$, $P = 0.383$).

Abundance of hypogeous sporocarps was greatest in June and August 2000 and lowest in August 2001 and June 2002

(Table 5). A total of eight species were identified, including five and four species from spring and summer collections, respectively. Sporocarp collections were dominated by *Rhizopogon ellenae*, *Elaphomyces granulatus*, and *Hymenogaster subolivaceus*. Across years (2000–2002), sporocarp biomass was equal between seasons (0.73 kg/ha for both June and August). Seasonal biomass of hypogeous fungal sporocarps was not significantly correlated with richness of fungal taxa in the diet of *G. sabrinus* ($r^2 = 0.103$, $P = 0.536$) or *N. speciosus* ($r^2 = 0.519$, $P = 0.106$). Seasonal rainfall (June–August 1999–2002) was positively correlated with the richness of fungal taxa in the diet of *N. speciosus* ($r^2 = 0.851$, $P = 0.032$) but not in the diet of *G. sabrinus* ($r^2 = 0.506$, $P = 0.306$).

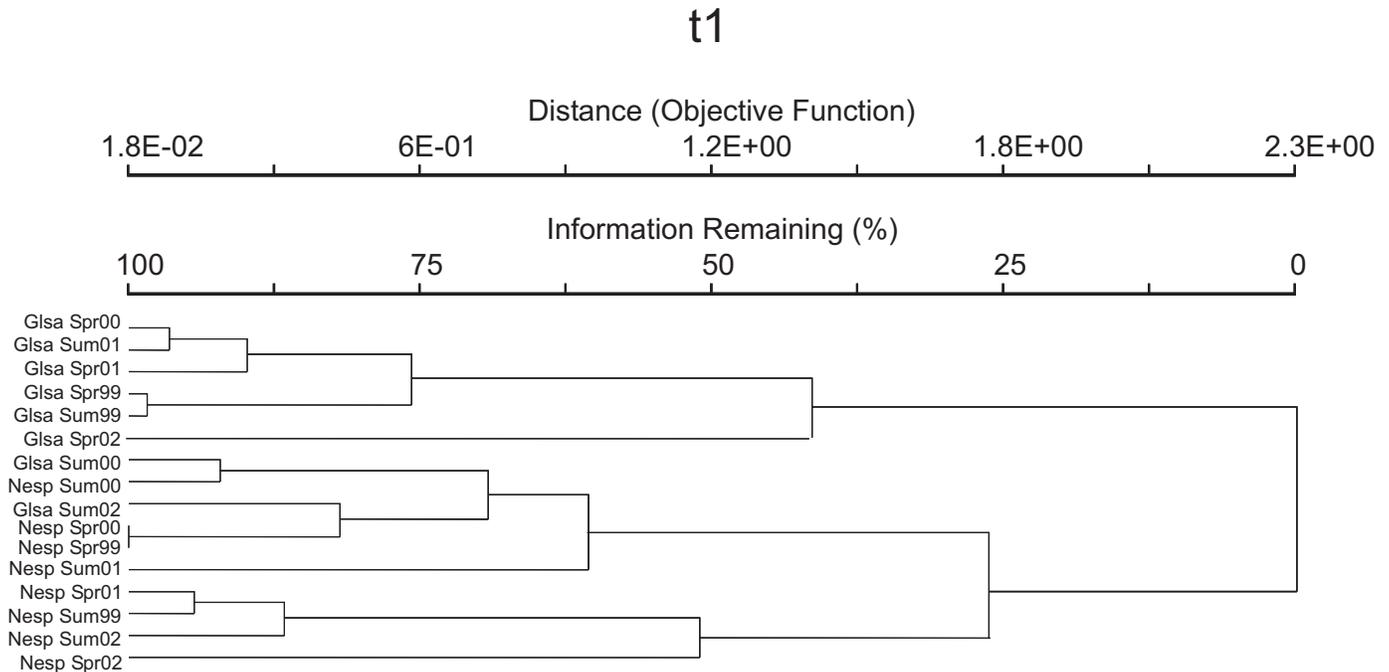
Cluster analysis based on Sorenson distances identified two major groups, one consisting of *G. sabrinus* diets from all periods except summer 2000 and 2002 and another consisting of all *N. speciosus* diets combined with *G. sabrinus* diets from summer 2000 and 2002 (Fig. 1). Within these major groups, there were no distinct seasonal or annual clusters for either squirrel species with the exception of *G. sabrinus* diets from 1999. Two fungal taxa were identified as significant contributors to the differences observed among the two major cluster groupings, *Gautieria* ($F_{[1,13]} = 30.804$, $P <$

Table 5. Biomass (kg/ha), frequency of occurrence (%), and species composition of hypogeous fungal sporocarps found during June and August 2000–2002 at Teakettle Experimental Forest.

Season and year	Biomass	Frequency	Species present*
June 2000	1.90	20	<i>Elaphomyces granulatus</i> (1.60), <i>Hymenogaster subolivaceus</i> (0.29), unknown species (0.01)
August 2000	1.31	12	<i>Leucophleps spinispora</i> (0.68), <i>Rhizopogon ellенаe</i> (0.58), <i>Hymenogaster idahoensis</i> (0.05)
June 2001	0.25	12	<i>Rhizopogon ellенаe</i> (0.17), <i>Hysterangium setchelli</i> (0.07), <i>Hydnotrya cerebriformis</i> (0.01)
August 2001	0	0	—
June 2002	0.06	4	<i>Rhizopogon ellенаe</i> (0.06)
August 2002	0.89	12	<i>Rhizopogon ellенаe</i> (0.86), <i>Martellia californica</i> (0.03) [†]

*Values in parentheses indicate the biomass of individual fungal species, and authority names are as follows: *Elaphomyces granulatus* Fr., *Hymenogaster subolivaceus* A.H. Smith, *Leucophleps spinispora* Fogel, *Rhizopogon ellенаe* A.H. Smith, *Hymenogaster idahoensis* A.H. Smith, *Hysterangium setchelli* Fischer, *Hydnotrya cerebriformis* Harkn., and *Martellia californica* Singer & A.H. Smith.

[†]Species is part of the Russulaceae.

Fig. 1. Clustering analysis of samples identified by squirrel species (*Glsa*, *Glaucomys sabrinus*; *Nesp*, *Neotamias speciosus*), season (Spr, Spring; Sum, Summer), and year (1999–2002) combinations. Samples are based on the proportion of fungal taxa consumed. Clustering used a Sorenson distance measurement and flexible β linkage.

0.0001) and *Gastroboletus* ($F_{[1,13]} = 23.830$, $P < 0.0001$). Frequencies of occurrence of *Gautieria* and *Gastroboletus* were high for the *G. sabrinus* group (*Gautieria*: 66% and *Gastroboletus*: 48%), but were only 7% for both fungal genera for the group consisting predominantly of *N. speciosus* diets. Horn's index of similarity expressed high degrees of dietary overlap between *G. sabrinus* and *N. speciosus* in all seasons and years (especially summer 2000 and 2002), with the exception of summer 2001 (low similarity) and spring 2002 (moderate similarity; Table 3).

Discussion

Seasonal and annual variation of fungi in diets

Diversity of fungi in the diets of *G. sabrinus* and *N. speciosus* lacked any seasonal patterns. Several fungal

taxa were more frequently consumed in the summer than in the spring (e.g., *Hymenogaster*, *Hysterangium*, *Leucogaster*, *Leucophleps*, *Rhizopogon*, Russulaceae) and in the spring than in the summer (e.g., *Gastroboletus*), but these trends were not consistent across years or squirrel species. In the central Sierra Nevada, *Rhizopogon* and *Leucophleps* were more frequent in autumn diets than in spring diets of *G. sabrinus* (Pyare and Longland 2001). Previous studies have reported seasonal variation in fungal diversity of squirrel diets (Hall 1991; Currah et al. 2000; Pyare and Longland 2001; Vernes et al. 2004), with greater diversity consumed in the summer than in the spring (Pyare and Longland 2001; Vernes et al. 2004). Vernes et al. (2004) suggested that squirrels probably consume fungi in proportion to their seasonal availability, with greater availability in the summer and autumn than in the winter or spring. At Teakettle, sea-

sonal availability (biomass, species richness) of hypogeous fungal sporocarps was similar overall between June and August, reflecting the marginal seasonal differences in fungal richness from squirrel diets.

Annual variation in the diversity and composition of consumed fungal taxa was high for both squirrel species at Teakettle. Several fungal taxa detected in diets in 1999–2001 were absent (e.g., *Leucophleps*, *Leucogaster*, *Hydnotrya*, *Hysterangium*), rare (e.g., Russulaceae, *Trappea*), or less common (e.g., *Hymenogaster*) in 2002. The absence of summer (June through August) rainfall during 2002 may have contributed to the relative paucity of fungal taxa during that year, since all other years received small amounts of precipitation (range: 0.64–1.98 cm). Summer precipitation at Teakettle was positively associated with the biomass of fungal sporocarps (Meyer and North 2005), as well as with the richness of fungal taxa in the diets of *N. speciosus*. Richness of fungal taxa in *N. speciosus* diets also was positively associated with seasonal and annual biomass of hypogeous fungal sporocarps, although this association was marginally insignificant ($P = 0.106$) based on our small sample size (2 seasons \times 3 years). Seasonal rainfall during spring and summer at Teakettle may reduce the richness of fungal taxa ingested by opportunistic consumers such as *N. speciosus* by limiting the abundance of fungal sporocarps. In contrast, the fungal diet of *G. sabrinus* was not associated with sporocarp abundance or seasonal rainfall, perhaps owing to the greater use of riparian than upland stands by *G. sabrinus* at Teakettle (Meyer 2003), where sporocarp abundance in riparian areas is not associated with summer rainfall or sporocarp biomass in upland stands (Meyer and North 2005).

The frequency of hypogeous fungi consumption was consistently high across seasons and years for both *G. sabrinus* and *N. speciosus*. Frequency of hypogeous fungi consumption for *G. sabrinus* was high during late-spring through autumn and ranged 90%–100% in the interior forests of western North America (Maser et al. 1978, 1985; Rosentreter et al. 1997; Pyare and Longland 2001). In contrast, the frequency of hypogeous fungi in *N. speciosus* diets at Teakettle (94%) was substantially higher than previously reported for northeast California (spring: 11% and summer: 42%; Tevis 1953) and the central Sierra Nevada (spring: 50% and autumn: 30%; Pyare and Longland 2001). Pyare and Longland (2001) documented higher frequencies of epigeous (80%–90%) than hypogeous fungi (30%–50%) in the diets of *N. speciosus* and *N. quadrimaculatus* in red fir forests of the central Sierra Nevada (e.g., the Lake Tahoe Basin), while hypogeous fungi were consumed in greater frequency than epigeous fungi (17%) at Teakettle. The drier forest stand conditions at Teakettle may have favored hypogeous fungi consumption by *N. speciosus*, owing to the brief period of epigeous sporocarp production (2 weeks to several days in the mid-spring) compared with hypogeous production (4–5 months from late-spring through autumn; M. Meyer, personal observation).

The frequency of fungal taxa in squirrel diets reflected the seasonal and annual abundance of sporocarps for some but not all hypogeous taxa. *Rhizopogon* was the most frequent fungal taxon both in squirrel diets and in sporocarp collections across years, indicating that this genus was consumed

opportunistically (Cazares et al. 1999). *Rhizopogon* is a frequent component of squirrel diets, as well as hypogeous sporocarp collections, throughout forests of western North America (Maser and Maser 1988; North et al. 1997; Cazares et al. 1999; Pyare and Longland 2001; Lehmkuhl et al. 2004). In contrast, *Elaphomyces* was absent from *G. sabrinus* and was only a minor component of *N. speciosus* diets during 2000 even though this genus dominated sporocarp collections in June 2000. *Elaphomyces granulatus* (the only species of *Elaphomyces* at Teakettle) often is consumed in low frequency relative to its abundance (North et al. 1997), perhaps owing to its low digestibility (Cork and Kenagy 1989) and nutrient content (Gronwall and Pehrson 1984). Other taxa that were frequently observed in squirrel diets (e.g., *Geopora*, *Melanogaster*, *Gautieria*; Tables 1, 2) were absent from sporocarp collections, possibly owing to the absence of sample quadrats located in riparian habitat where these genera occur in greater abundance than in non-riparian sites (Meyer and North 2005).

Similarity of *G. sabrinus* and *N. speciosus* diets

We observed a high degree of similarity in most fungal taxa consumed by *G. sabrinus* and *N. speciosus* (Table 4). In nearly all sampling periods, both squirrel species consumed similar proportions of the most abundant fungal taxa, including *Rhizopogon*, *Melanogaster*, *Geopora*, and *Hymenogaster*. However, both *Gautieria* and *Gastroboletus* were frequently found in the diet of *G. sabrinus* but were uncommon in the diet of *N. speciosus*. In the cluster analysis, both fungal taxa were significant variables contributing to the separation of *G. sabrinus* and *N. speciosus* into two distinct dietary groups (with the exception of *G. sabrinus* summer 2000 and 2002 diets). In the central Sierra Nevada, *Gastroboletus* was frequently consumed by *G. sabrinus* but was absent from the diets of *N. speciosus* and *N. quadrimaculatus*. In western Washington, *Gautieria* was common in the diet of *G. sabrinus* but was rare in that of Townsend's chipmunk (*Neotamias townsendii* (Bachman, 1839); Carey et al. 2002). In the southern Cascade Range of Oregon, *Gautieria* was more frequently consumed by *G. sabrinus* than by the Siskiyou chipmunk (*Neotamias siskiyou* (A.H. Howell, 1922); Cazares et al. 1999). In controlled feeding trials, *G. sabrinus* preferred *Gautieria* to other hypogeous fungal taxa (Zabel and Waters 1997). Results from our study and others indicate that *N. speciosus* may not share the same strong preference for *Gautieria*.

Strong overlap in consumed fungal taxa between *G. sabrinus* and *N. speciosus* indicates that diets were more similar than previously reported for *G. sabrinus* and a chipmunk species. In the central Sierra Nevada, *G. sabrinus* and *N. speciosus* (combined with *N. quadrimaculatus*) shared 19% of fungal taxa in their diets, while flying squirrels and Douglas squirrels (*Tamiasciurus douglasii* (Bachman, 1839)) shared 56% of taxa (Pyare and Longland 2001). In western Washington, 67% of fungal genera were shared between *G. sabrinus* and *N. townsendii* (Carey et al. 1999), while the same percentage of taxa in winter diets was shared between *G. sabrinus* and red squirrels (*Tamiasciurus hudsonicus* (Erxleben, 1777)) in northeastern Alberta (Currah et al. 2000). Interestingly, similarity in consumed fungal taxa between *G. sabrinus* and *T. hudsonicus* in New Brunswick during spring and summer

was greater (Horn's index: 0.84–0.94; Vernes et al. 2004) than between *G. sabrinus* and *N. speciosus* in this study (0.26–0.77).

Across seasons and years, richness of consumed fungi taxa was marginally greater for *G. sabrinus* than for *N. speciosus*, supporting the notion that the diversity of fungal taxa was greater in the diet of a fungal specialist than in that of a dietary generalist. In old-growth, red fir forests of the central Sierra Nevada, *G. sabrinus* consumed a greater number of hypogeous fungal genera than did *N. speciosus* and *N. quadrimaculatus* (Pyare and Longland 2001). In old-growth and managed stands of western Washington, generic richness of fungi also was greater in the diet of *G. sabrinus* than in that of *N. townsendii* (Carey et al. 1999, 2002). In coniferous forests of Oregon, the richness of fungal taxa was greater in the diets of *G. sabrinus* than in that of the yellow-pine chipmunk (*Neotamias amoenus* J.A. Allen, 1890) or *N. townsendii* (Maser et al. 1978). However, richness of fungal taxa was similar between *G. sabrinus* and *T. hudsonicus* in old-growth, mixed-wood forests of New Brunswick (Vernes et al. 2004).

Implications for the dispersal of fungal spores

Frequent ingestion of hypogeous fungal spores by both *G. sabrinus* and *N. speciosus* has several important implications for the dispersal of ectomycorrhizal spores in mixed-conifer forests of the Sierra Nevada. *Glaucomys sabrinus* was frequently captured in riparian and unharvested, closed-canopy, old-growth forest stands at Teakettle where they often were more abundant than *N. speciosus* (M. Meyer, personal observation). In contrast, *N. speciosus* is a habitat generalist that is equally abundant among old-growth, intensively thinned, and burned forest stands at Teakettle (Meyer 2003). Differences in habitat and microhabitat use by these two species may increase the establishment potential of ectomycorrhizal spores to heterogeneous forest stands that are patchy and have experienced different management and disturbance legacies (Pyare and Longland 2001; Carey et al. 1999). Additionally, differences in the taxonomic composition of fungal sporocarps by both squirrel species have the potential to enhance the dispersal of a greater number of fungal taxa in Sierra Nevada mixed-conifer forests. Taxa such as *Gautieria* and *Gastroboletus* may be more frequently dispersed by *G. sabrinus*, while *Elaphomyces* and *Cortinarius* may be more frequently dispersed by *N. speciosus*.

Fungi are an important part of the diet of mycophagous small mammals (Maser et al. 1978; Pyare and Longland 2001) and a key ecosystem component in forests of the Sierra Nevada (North 2002). Despite their importance in forest management plans of other geographic regions (36% of species of concern in Washington, Oregon, and Northwest California; Castellano et al. 1999), fungi have received little attention in management plans of the Sierra Nevada (0% of species of concern are fungi; Sierra Nevada Forest Plan Amendment 2004), largely owing to the lack of sufficient information on the ecology and distribution of fungi in this range. Mycological research in the Sierra Nevada is sorely needed to fill this gap in knowledge and assist in the management of fungi, particularly hypogeous taxa that are important components of mycophagous small-mammal diets.

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