Cynthia J. Zabel and **Jeffrey R. Waters**, U.S. Forest Service, Pacific Southwest Research Station, 1700 Bayview Drive, Arcata, California 95521

Food Preferences of Captive Northern Flying Squirrels from the Lassen National Forest in Northeastern California

Abstract

Hypogeous sporocarps of mycorrhizal fungi (truffles) are a common food of northern flying squirrels (*Glaucomys sabrinus*) and many other species of small mammals. Forest management practices and natural disturbances can affect both total amounts and species composition of truffles. We conducted cafeteria-style feeding trials to compare preferences of northern flying squirrels captured in the Lassen National Forest in northeastern California among sporocarps of 5 species of fungi (3 truffle species and 2 species of secotioid fungi), 2 species of lichens, and fir (*Abies magnifica* and *A. concolor*) seeds. Feeding trials were performed on 7 male squirrels for 4 consecutive nights. Mean proportion of food eaten varied significantly among the 3 truffle species, between the 2 species of secotioid fungi, and between the 2 lichen species. Mean proportion of food eaten was greatest for 2 of the truffle species, followed by the lichen *Bryoria fremontii*. These results indicate that northern flying squirrels preferred truffles over certain types of other naturally occurring foods, and that preference varied significantly among sporocarps of different fungal species. Natural disturbance and forest management that alter the species composition of fungal sporocarps are likely to affect the availability of foods preferred by northern flying squirrels.

Introduction

Numerous species of small mammals feed on hypogeous sporocarps of mycorrhizal fungi (hereafter referred to as "truffles") in temperate and tropical forests throughout the world (e.g., Tevis 1953, Fogel and Trappe 1978, Maser et al. 1978, Taylor 1992, Johnson 1994, Janos et al. 1995). Some species, such as the northern flying squirrel (*Glaucomys sabrinus*), California red-backed vole (*Clethrionomys californicus*) (Ure and Maser 1982), and various species within the marsupial family Potoridae (Taylor 1992, Claridge and Cork 1994, Johnson 1994) are highly mycophagous and feed on truffles as one of their primary food sources. Although sporocarps are consumed, spores are viable after passage through small mammal digestive tracts (Trappe and Maser 1977, Cork and Kenagy 1989, Claridge et al. 1992), and Cork and Kenagy (1989) showed that passage through the digestive tract of a species of ground squirrel enhanced spore germination. Because most species of fungi that produce hypogeous sporocarps eaten by small mammals are thought to be mycorrhizal, mycophagous small mammals contribute to the maintenance of mycorrhizal symbioses (Trappe and Maser 1977, Maser et al. 1978).

In a previous study we evaluated associations between northern flying squirrel density and forest structure in fir (*Abies* spp.) stands in the Lassen National Forest in northeastern California (Waters and Zabel 1995). We found truffles in each of the 155 flying squirrel fecal samples examined, and flying squirrel density was correlated with frequency of hypogeous sporocarps across the 12 stands in which we sampled. Lichens, unknown vegetative matter, spores from epigeous fungi, pollen from conifer staminate cones, insect parts, and seed parts were also observed in fecal samples. In another study, we found significant association between thinning level (heavily thinned, moderately thinned, and unthinned) and frequencies of the 5 most common truffle genera, suggesting that thinning led to changes in the composition of truffle species (Waters et al. 1994). We also found significant association between stand age (old-growth and mature stands that originated after wildfire) and frequencies of truffle species, suggesting that disturbance had long-lasting effects on the composition of truffle species (Waters et al. In Press). Other studies have also shown that composition of hypogeous sporocarps varied among stands with different management or natural disturbance histories (Vogt et al. 1981, Luoma et al. 1991, North et al. In Press). Because forest management alters species composition of fungal sporocarps, we wanted to know whether palatability varied among sporocarps of different fungal species for a common, mycophagous small mammal. We designed this study to determine whether northern flying squir-

rels preferred sporocarps of certain fungal species over others, and secondarily to compare preferences of flying squirrels between fungal sporocarps and other naturally occurring food types.

Methods

Flying squirrels were trapped 4-5 August 1994 in 2 old-growth (>200 years) fir stands in Swain Mountain Experimental Forest, located in Lassen National Forest in northeastern California. Only males were kept for the experiments to control for possible sex effects in food preferences (e.g., the sensory acuity of females may vary according to reproductive status). Squirrels were transported to Humboldt State University in Arcata, California, where they were housed individually in 1.0x1.0x1.5-m outdoor cages. Cafeteria-style experiments were conducted in 2 1.2x1.2x1.0-m cages that had wooden frames and 1-cm hardware cloth sides. Lids were made of clear plexiglass. A wooden tray served as the floor of each cage. Trays were filled to a depth of 6-7 cm with peat moss. The 2 cages were located in separate indoor rooms that lacked windows.

Squirrels were allowed to acclimate to captivity for 2 weeks before experiments began. During the acclimation period, squirrels were fed samples of the food types used during the experiments for approximately 30 minutes each night while in the test cage. Beginning the day before the experiments began, animals were maintained on a reduced diet of rat chow, apples, and water. They were weighed daily to ensure that their weight did not drop below 90% of their capture weight.

Experiments began shortly after sunset when squirrels were moved from their outdoor cages into the test rooms, which were each illuminated with a red light. Order of testing and test room were randomly determined each night. Flying squirrels entered the center of the cage through a plastic tube (8 cm in diameter). An observer recorded behavioral observations with a tape recorder from a blind 1 m from the test cage. Seven squirrels were tested for 45 minutes each night for 4 consecutive nights (17-20 August 1994).

Preferences of flying squirrels were compared among 3 types of food that are available to flying squirrels in the Lassen National Forest: fungal sporocarps, epiphytic lichens, and fir seeds. Fungal sporocarps and lichens were collected in old-growth and mature stands within Swain Mountain Experimental Forest. Fir (*A. concolor* and *A. magnifica*) seeds were obtained from a U.S. Forest Service nursery in Placerville, California. We used sporocarps of 5 species of fungi that were found in sufficient quantities at the time of sampling (14-16 August 1994). Sporocarps were found by raking through the organic layers and upper mineral soil in 4-m^2 circular plots (1.13-m radius) randomly located throughout forest stands. The 5 species were *Gautieria monticola*, *Alpova trappei*, *Gymnomyces abietis*, *Endoptychum depressum*, and *Arcangeliella lactarioides*. *Gautieria monticola*, *Alpova trappei*, and *Gymnomyces abietis* are truffle species; sporocarps lack gills and a stipe and are found below ground. *Endoptychum depressum* and *Arcangeliella lactarioides* are secotioid fungal species, which are considered evolutionary intermediates between fungi that produce epigeous sporocarps and truffles and have morphological and fruiting characteristics of both groups; sporocarps have convoluted gills that are covered by a veil, a reduced stipe, and are found both at the ground surface and below ground. The 2 lichens were *Letharia vulpina* and *Bryoria fremontii*, which were 2 of the most common epiphytic lichens within Swain Mountain Experimental Forest. Fungal sporocarps and lichens were kept in a refrigerator until used in the preference tests.

Size of food samples was standardized across foods and tests; samples were 2-3 cm in diameter. All food samples were weighed before and after each test to determine proportion of food eaten. Each food sample was placed in a randomly assigned grid cell across the tray of the feeding cage before the squirrel entered the cage. Truffles were buried 2-3 cm, and all other samples were placed on top of the peat moss. Fir seeds were placed in a petri dish 4 cm in diameter that was buried so it was level with the peat moss. The peat moss was thoroughly mixed with a rake after each experiment and was changed nightly.

Data Analysis

We compared 3 measures of food preference: (1) proportion of food eaten, (2) number of tests in which food was at least partially eaten, and (3) rank order food was first eaten. Any food types not eaten were ranked last. We used the Spearman rank correlation coefficient for each of the 3 pairwise comparisons of these measures as an index

of similarity. The number of tests in which a food was at least partially eaten was averaged across the 7 squirrels, and proportion of food eaten and rank order food was first eaten were averaged across the 4 nights and 7 squirrels. Ranked correlations (n = 8 foods) were high (r_S = 0.98 between proportion of food eaten and number of tests food was at least partially eaten, r_S = -0.95 between proportion of food eaten and rank order food was first eaten, and r_S = -0.98 between number of tests food was at least partially eaten and rank order food was first eaten), indicating the 3 measures provided similar information. We used the proportion of food eaten (averaged across the 4 nights) to test for a difference in food preference among the 8 foods using a randomized complete-blocks (each squirrel was a block) design analysis of variance (ANOVA). Unplanned multiple comparisons were performed using the Ryan-Einot-Gabriel-Welsch multiple-range test (SAS Institute Inc. 1989:947). Roa (1992) and Manly (1993) proposed using multivariate analyses of data from food-preference experiments where foods are presented simultaneously because of the lack of independence among foods. We decided to use a more simple univariate approach because the food samples provided were small (2-3 cm in diameter), so consumption of 1 food probably had little effect on consumption of other foods.

Results and Discussion

Mean proportion of food eaten varied significantly among the 8 foods ($F_{7, 42}$ = 31.75, P < 0.001). Multiple comparisons indicated that the truffle species *Gautieria monticola* was eaten significantly more than the truffle species *Gymnomyces abietis*, and the secotioid species *Endoptychum depressum* was eaten significantly more than the secotioid species *Arcangeliella lactarioides* (Figure 1). Among the 5 species of fungi, mean proportion of food eaten ranged from 0.90 (s.e. = 0.05) for *Gautieria monticola* sporocarps to 0.11 (s.e. = 0.04) for *Arcangeliella lactarioides* sporocarps.

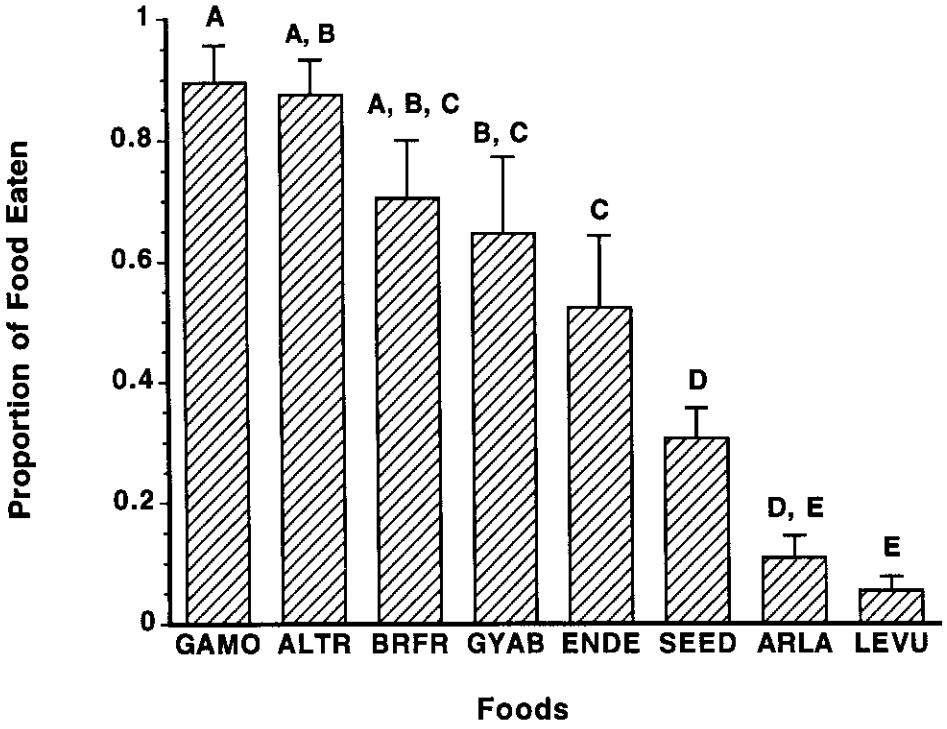

Figure 1. Means and standard errors of proportion of food eaten (averaged across a 4-night period) by 7 captive, male northern flying squirrels during cafeteria-style feeding trials. Foods were *Gautieria monticola* sporocarps (GAMO), *Alpova trappei* sporocarps (ALTR), the lichen *Bryoria fremontii* (BRFR), *Gymnomyces abietis* sporocarps (GYAB), *Endopytchum depressum* sporocarps (ENDE), fir seeds (SEED), *Arcangeliella lactariodes* sporocarps (ARLA), and the lichen *Letharia vulpina* (LEVU). Foods with the same letter did not differ significantly using the Ryan-Einot-Gabriel-Welsch multiple-range test.

The 3 truffle species were consumed more than the 2 secotioid species, which is consistent with results of other studies that showed hypogeous sporocarps were more common in the diets of mycophagous small mammals than were epigeous sporocarps (Maser et al. 1978, 1986, Ure and Maser 1982, Maser et al. 1985, Maser and Maser 1987, Taylor 1992). Our results are also consistent with 3 studies that found that spores of *Gautieria* and the *Rhizopogon* group, which includes the genus *Alpova* (Castellano et al. 1989), were the most common truffle spores identified in northern flying squirrel stomachs and fecal pellets in Oregon and California (Maser et al. 1985, Maser et al. 1986, Hall 1991). Hall (1991), whose study was conducted in the northern Sierra Nevada not far from our study area, found that *Gautieria* spores were found in 87% of 107 flying squirrel fecal pellets and stomachs examined, the *Rhizopogon* group in 81%, and the *Martellia* group, which includes the genus *Gymnomyces* (Castellano et al. 1989), in 17%. Maser et al. (1985) also found that the *Martellia* group was less common than *Gautieria* and the *Rhizopogon* group, and Maser et al. (1986) did not record the presence of the *Martellia* group.

The lichen *Bryoria fremontii* was ranked third in mean proportion of food eaten. The relatively high preference for this lichen is consistent with dietary studies, which have shown that lichens were common in the diets of northern flying squirrels (McKeever 1960, Maser et al. 1985, Maser et al. 1986, Hall 1991). These studies, however, showed that lichens were much less common in the summer diets of flying squirrels than the winter diets, suggesting that lichens were eaten primarily when other foods like truffles were unavailable. Because our study was only conducted during the summer, we cannot assess potential differences in food preferences among seasons. The small amounts of the lichen *Letharia vulpina* eaten is not surprising because this species contains vulpinic acid, which is thought to be toxic to mammals (Smith 1921, Rundel 1978).

Flying squirrels ate sporocarps of 4 of the 5 species of fungi and one lichen species significantly more than fir seeds. This is consistent with dietary studies, which have not found conifer seeds to be common in the diets of northern flying squirrels. Brink and Dean (1966) found that red squirrels (*Tamiasciurus hudsonicus*) in Alaska could maintain weight on a diet of white spruce (*Picea glauca*) cones, but northern flying squirrels could not. In our study, fir seeds were not presented on the cone as they would be found under natural conditions. Because the squirrels did not have to extract seeds from the cone, however, the energetic value of the seeds was theoretically greater than the energetic value of fir seeds under natural conditions.

We showed that preference varied significantly among the 8 foods tested, but we do not know how the nutritional and energetic values of these foods varied. Cork and Kenagy (1989) found that the nutritional value of 1 species of truffle (*Elaphomyces granulatus*) was low for the ground squirrel *Spermophilus saturatus* because digestibility of the sporocarps was low. They hypothesized that truffles in general have relatively low nutritional value for small mammals but are commonly consumed because truffles are seasonally abundant and highly detectable due to the strong odors they develop when mature. Claridge and Cork (1994), however, found that the energetic values of 2 truffle species were high for a forest-dwelling marsupial (*Potorous tridactylus*) in Australia. Because of their high water content, fungal sporocarps may be important during certain periods or in certain areas as a source of water (Fogel and Trappe 1978). Additional research will be needed to determine the nutritional values of different truffle species for different species of mycophagous small mammals.

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