

OBSERVATIONS OF NORTHERN FLYING SQUIRREL FEEDING BEHAVIOR: USE OF NON-TRUFFLE FOOD ITEMS

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ABSTRACT—In the Pacific Northwest, the northern flying squirrel, *Glaucomys sabrinus*, consumes sporocarps of a wide variety of hypogeous mycorrhizal fungi (truffles). Numerous other foods are also consumed but are not well characterized by fecal pellet analysis either because they are more fully digested (seeds, nuts, fruits, vegetation) or because of the similarity among spore types (lichen photobionts, epigeous fungi). Thus, observations of squirrel foraging are important in characterizing non-truffle dietary components. As part of a trapping and telemetry study, we observed *G. sabrinus* foraging on 63 occasions; 34 were observations of non-truffle consumption. These foods included epigeous fungi, fruits and seeds, and conifer seedlings. We hypothesize *G. sabrinus* may consume more non-truffle foods than is indicated by fecal pellet analysis, and that such foods may be important nutritional supplements to a low-quality diet as well as substitutes for truffles in times or places of low truffle abundance. By availing themselves of other food sources, *G. sabrinus* may persist in otherwise marginal habitats, while also contributing to the dispersal of a wide diversity of fungi and increasing genetic diversity of fungal and microbial species.

The northern flying squirrel, *Glaucomys sabrinus*, is an inhabitant of coniferous and mixed-deciduous forests of North America. Studies of food habits of *G. sabrinus* in the Pacific Northwest have consistently reported the predominance of hypogeous fungi (truffles) in the diet (McKeever 1960; Fogel and Trappe 1978; Maser and others 1978a, 1986; Gunther and others 1983; Maser and Maser 1988; McIntire and Carey 1989; Hall 1991; Carey 1995; Waters and Zabel 1995). In the Pacific Northwest, *G. sabrinus* consumes a wide variety of truffle species, with up to 20 genera (representing 40 or more species) having been identified from single squirrel populations (Maser and Maser 1988; Carey 1995; Carey and others 1996).

In areas of heavy snowfall, fruticose lichens (*Alectoria*, *Bryoria*, *Letharia*, *Usnea*) are a large part of the diet of *G. sabrinus* (McKeever 1960; Maser and others 1985, 1986; Hall 1991). Waters and Zabel (1995) also reported high frequency of lichens in fecal pellets from summer-trapped flying squirrels in an area of heavy winter snow, but did not specify lichen taxa. Where snow cover is light or infrequent (including northwest Oregon, the southern Coast Range of Oregon, low elevation portions of the Olympic Peninsula, and the Puget Trough), *G. sabrinus* shows little evi-

dence of lichen consumption (Maser and others 1978a, 1986; Carey 1995; Carey and others 1996).

In the Pacific Northwest, other foods have been noted, generally with low relative frequency and usually in broad categories: epigeous fungi, insects or insect parts, seeds, and pollen from the staminate cones of conifers (Maser and others 1985, 1986; Hall 1991; Waters and Zabel 1995). Outside of the Pacific Northwest, similar non-truffle food types have been reported in *G. sabrinus* diets "in amounts suggesting substantial and frequent ingestion" (Weigl and others 1992, p75). Though flying squirrels clearly consume a variety of non-truffle foods (Weigl 1978; Wells-Gosling and Heaney 1984; Maser and others 1985, 1986; Hall 1991; Weigl and others 1992; Waters and Zabel 1995), these foods remain only broadly characterized.

Use of ancillary foods is not well documented due to difficulty in identifying digested remains, possible minor or sporadic consumption, or infrequent observations of foraging. Some foods such as nuts, berries, and seeds (with the exception of some seed integuments) are highly digestible and are rarely identifiable in feces (Johnson and others 1983, McIntire and Carey 1989). In contrast, fungal spores pass through the gut intact and

viable (Trappe and Maser 1976; Claridge and others 1992); most truffle genera and many truffle species are identifiable based on microscopic spore characters (Castellano and others 1989). The similarity of many epigeous fungal spores, however, typically limits their identification to a broader taxon, or simply to epigeous fungi.

Because *G. sabrinus* is nocturnal, opportunities to observe foraging are rare. However, during our 5 yr of intensive study, we have observed them feeding on truffle and non-truffle foods. Many non-truffle foods are indiscernable in fecal pellets except as amorphous plant tissue (Carey 1995; Waters and Zabel 1995), or as unidentified fungal spores (Maser and others 1985, 1986; Waters and Zabel 1995; Colgan and others 1997). Here, we describe use of dietary resources by *G. sabrinus* that are not well characterized in the literature, and we discuss the potential importance of these foods in the diet of *G. sabrinus*.

STUDY AREA

The study area included the Forest Ecosystem Study site on the Fort Lewis Military Reservation in the southern Puget Trough in western Washington (Carey and others 1996), and the Capitol Forest just southeast of the Puget Trough. Fort Lewis stands were predominantly 50 to 70 yr-old, competitive-exclusion stage or understory reinitiation stage (Oliver and Larson 1990, Carey and Curtis 1996) Douglas-fir (*Pseudotsuga menziesii*) stands that regenerated naturally following wide-scale clear-cutting in the 1920s and 1930s. Western red-cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*) and black cottonwood (*Populus trichocarpa*) were minor components, comprising <5% of total stems. Terrain was flat to rolling and elevation was 100 to 140 m.

The Capitol Forest site contained more hardwoods than Fort Lewis. The stand was dominated by red alder and bigleaf maple in the overstory, conditions resulting from earlier selective removal of large diameter Douglas-fir. In addition, Douglas-fir, western hemlock, and western red-cedar were secondary constituents of the Capitol Forest stand. The conifers were primarily smaller diameter trees that established following previous logging entries. The stand had a SW aspect, 10 to 20% slope, and elevation was 250 to 300 m. The Capitol Forest site was in the nichediversification stage of forest development (Carey and Curtis 1996).

METHODS

We trapped *G. sabrinus* in spring and fall, from fall 1991 through fall 1996 at Fort Lewis, and from fall 1995 through fall 1996 at Capitol Forest. Fall trapping dates varied from late September through early December; spring trapping always occurred in May. Trapping methods followed Carey and others (1991). All captured animals were released daily and behavior following trap release was documented.

Adult *G. sabrinus* were fitted with radio transmitters. Nocturnal behavior was studied with telemetry from fall 1993 to summer 1995 at Fort Lewis. Most tracking occurred November through March and May through August. Squirrels were tracked continuously at close range (20 to 40 m) from when they left the den until they returned, or for a minimum of 3 hr. Movement was recorded as successive locations in space and time. Location was determined by triangulation at close range during periods of localized squirrel activity. When *G. sabrinus* were observed feeding, food items were identified when possible.

RESULTS

Forty-three individual *G. sabrinus* were observed foraging 63 times (Table 1). Twenty-nine were visual observations of truffle consumption (21 after release from traps, 8 during tracking), and 34 were of other food consumption (21 trap release, 13 tracking).

We saw 21 *G. sabrinus* eat mycorrhizal or saprophytic epigeous fungi on 25 occasions. In 17 cases fungi were identified (Table 1): these were *Entoloma* sp., puffballs (*Lycoperdon perlatum*), *Pholiota squarrosoides*, oyster mushrooms (*Pleurotus ostreatus* and *P. porrigens*), the deer mushroom (*Pluteus cervinus*), a resupinate *Poria* sp., and *Russula* sp. (*R. brevipes* and *R. xerampelina*). *Pleurotus ostreatus* and *Russula* spp. were the most frequently eaten epigeous fungi.

On several occasions, *G. sabrinus* ate *Russulas* by first breaking the caps off the stalks so that the tops lay on the ground, underside exposed. Squirrels then scraped gills off with their lower incisors. Gills were sometimes preferentially removed from oyster mushrooms in the same manner. At other times, squirrels took bites from stalks or caps or both when feeding on mushrooms. On 1 occasion after trap release, a female *G. sabrinus* was observed sitting under a large log eating *Poria* sp. She twisted her upper body to face the mat-like fungus growing on the underside of the log, pulled off small pieces of

TABLE 1. Phenology and observed use of food items consumed by *Glaucomys sabrinus*. Numerals in cells are the number of observations after trap release (Trap), or during tracking (Track), and total by month. Shaded areas indicate times of predicted food availability (phenology from USDA 1974; Arora 1986; Burns and Honkala 1990a, 1990b; and personal observations).

| Food type | Trap | Track | Month | | | | | | | | | | | |
|--|-----------|-----------|----------|----------|----------|----------|-----------|----------|----------|----------|----------|----------|-----------|----------|
| | | | J | F | M | A | M | J | J | A | S | O | N | D |
| Fungi | | | | | | | | | | | | | | |
| <i>Entoloma</i> sp. ^a | 1 | | | | | | | | | | | | 1 | |
| <i>Lycoperdon perlatum</i> ^a | 1 | | | | | | | | | | | | 1 | |
| <i>Pholiota squarrosoides</i> ^a | 1 | | | | | | | | | | | | 1 | |
| <i>Pleurotus</i> spp. ^a | 3 | 3 | | 1 | 1 | 1 | 1 | | | | | 1 | | 1 |
| <i>Pluteus cervinus</i> ^a | 1 | | | | | | | | | | | 1 | | |
| <i>Poria</i> sp. ^{a,b} | 1 | 1 | | 1 | 1 | | | | | | | | | |
| <i>Russula</i> spp. ^a | 5 | | | | | | | | | | | | | 5 |
| Unidentified mushroom ^a | 4 | 4 | | 2 | | | | | 1 | | | 1 | 2 | 2 |
| Truffles ^a | 21 | 8 | 1 | | 1 | 1 | 12 | 3 | 4 | 1 | 2 | 3 | 1 | |
| Non-fungi | | | | | | | | | | | | | | |
| Douglas-fir seed ^c | | 1 | | | | | | | 1 | | | | | |
| Douglas-fir seedling ^a | 2 | | | | | | 1 | | | | | 1 | | |
| Maple seed ^a | 1 | 1 | | | | | | | | | | | 1 | 1 |
| Poplar catkin ^c | | 3 | | 1 | 2 | | | | | | | | | |
| Salal fruit ^a | 1 | | | | | | | | | | | 1 | | |
| Total Observations | 42 | 21 | 2 | 5 | 5 | 3 | 14 | 4 | 7 | 1 | 4 | 9 | 10 | 4 |

^aAnimal observed consuming food.

^bOne of a number of resupinate, wood-decomposing fungi.

^cFood detritus observed falling from squirrel location.

fungus with her forefeet, and returned to an upright sitting position to eat. This motion was repeated several times.

Glaucomys sabrinus were also seen eating non-fungal foods. Five observations were made of 4 individuals. Two squirrels foraged in the crowns of bigleaf maples and ate the seeds from samaras. After trap release, 1 squirrel moved among the outer branches of 2 maple trees to feed on seed clusters; the squirrel spent approximately 6 min in each tree. During tracking, another squirrel was observed eating seed from a fallen maple tree. At another time, this same squirrel was seen eating 4 to 5 salal (*Gaultheria shallon*) fruits after trap release. When foraging for salal fruits, the squirrel moved along the ground holding its head up until a berry was located. It then pulled the berry to its mouth with its forefeet and bit it from the branch. Two different squirrels fed on the needles of Douglas-fir seedlings after being released from traps. One ate the top whorls of 6 seedlings, sometimes sniffing at other seedlings but not eating them. The 2nd squirrel bit the top whorl from 1 seedling. Both squirrels found and consumed truffles during these seedling-eating episodes.

During 4 tracking observations, squirrels were observed where food was available and food detritus fell from squirrel locations, but observers did not see food being consumed. A male *G. sabrinus* was active for 36 min in a black cottonwood which had leaf buds and staminate catkins present. Vegetative debris fell from where the squirrel was heard moving in the canopy. Two nights later the same squirrel and another male were simultaneously located in the same tree for 40 min. Radio signals indicated sporadic movement, crackling sounds were heard, and small pieces of debris, including catkin fragments, fell from the canopy. On another occasion, cone stems and scales fell from a Douglas-fir where a squirrel was located for 36 min (Table 1).

DISCUSSION

The literature shows truffles and lichens predominate the diet of *G. sabrinus* in the Pacific Northwest but that numerous other foods are consumed as well. However, the value of these ancillary foods to *G. sabrinus* remains unknown. Though fecal pellet analysis is the standard method for evaluating small mammal diets, there are limitations

to identifying and quantifying digested remains.

Analysis of fecal contents may underestimate squirrel use of some truffle taxa, epigeous fungi, and other non-truffle foods. Such analyses usually report the relative frequency of each spore type, but the amount of indigestible spores is not a direct measure of digestible tissue consumed. For example, use of truffle or gasteromycete genera such as *Elaphomyces*, *Radiigera*, *Lycoperdon*, and *Scleroderma* may be underestimated because small mammals typically eat only the outer, non-spore containing tissue (Trappe and Maser 1977, Colgan and others 1997, personal observation). Because *G. sabrinus* eat mushroom stalks, caps, and gills, use of epigeous fungi could be underestimated in like manner. Fecal pellet analysis likely underestimates use of other highly digestible foods such as large seeds and fruits as well. The fungal families Coprinaceae, Cortinariaceae, Agaricaceae, Boletaceae, and Russulaceae have been reported in *G. sabrinus* diets (A. B. Carey, unpublished data), and because these families contain difficult to distinguish hypogeous and epigeous genera (Castellano and others 1989), the relative contribution of each type is unknown.

For these reasons, fecal pellet analyses may not sufficiently describe the importance of some foods. Although non-truffle food items are probably consumed in smaller quantities than truffles, they could be of more value to *G. sabrinus* than relative frequency indicates. Seeds, fruits, mushrooms, and other foods could be important as nutritional supplements, or as alternative foods when or where truffles become scarce.

Because of the low digestibility reported for individual truffle species (Cork and Kenagy 1989; A. W. Claridge, Canberra, Australia, pers. comm.), there is some doubt that a diet consisting solely of truffles would provide sufficient nourishment to *G. sabrinus*. While truffles are most likely the caloric staple for the flying squirrel in the Pacific Northwest, the more highly digestible seeds, fruits, nuts, and insects could be occasional, but nutritionally significant additions to the diet of *G. sabrinus*.

Fruiting of a variety of non-truffle foods coincides with periods of reduced truffle availability, and thus may stabilize an otherwise fluctuating food supply. In the Pacific Northwest, annual and seasonal truffle abundance varies widely. Typically, peak abundance occurs in the spring (April to June) and, to a lesser extent, fall (October to November); conversely, truffles may be scarce at times (Fogel 1976; Fogel and Hunt 1979; Hunt and Trappe 1987; Luoma and others

1991). Epigeous fungi, typically most abundant during late summer and early fall, could thus be seasonally important contributions to the squirrel diet; Maser and others (1986) and Waters and Zabel (1995) provide support for this view by showing relatively high use of epigeous fungi during that season. Alternate foods could be critical dietary elements during periods of low truffle abundance, and may contribute to squirrel survival in habitats that would be unsuitable if squirrels were dietarily restricted to truffles.

Both den sites and truffle abundance have been suggested as limiting factors for *G. sabrinus* in second-growth forests (Carey 1995; Waters and Zabel 1995; Carey and others 1997). Food availability as a limiting factor was also suggested by Ransome and Sullivan (1997). They showed that densities of *G. sabrinus* increased, and were significantly higher than both control and old-growth sites, after supplemental feeding of sunflower seeds in second-growth stands. Non-truffle foods, especially seeds, nuts, and fruits, are infrequent in closed-canopy, competitive-exclusion forests, and the lack of these foods may also be a factor limiting flying squirrel populations.

By consuming a variety of non-truffle foods as well as truffles, *G. sabrinus* could forage in areas with more brush and hardwood species and in young forest stands—stands typified by fewer truffle species and less dry weight production than more mature forests (Amaranthus and others 1994; Clarkson and Mills 1994). In the process, *G. sabrinus* would ensure dispersal of a diversity of fungal taxa, help maintain genetic diversity for mycorrhizal fungal species (Maser and others 1978b) and other soil microbes (Li and others 1986), and contribute to the increase in truffle diversity that is associated with forest development and canopy closure (Amaranthus and others 1994).

Some fungi we report being eaten were saprophytes found exclusively on hardwoods (*Pleurotus ostreatus*, *Pholiota squarrosoides*)—a substrate typically scarce in even-age and competitive-exclusion phase, managed conifer forests. Foods such as maple samaras, hardwood catkins, and fleshy fruits are also infrequent under such conditions. Through forest management practices that incorporate provisions for minimizing competitive-exclusion conditions and for retaining hardwoods and shrubs (Carey and Curtis 1996), *G. sabrinus* (and the mustelids, owls, and other predators that feed on them) should benefit from the associated

associated diversity of catkin-, seed-, fruit-, and nut-bearing plants, and their fungal mutualists. The diversity of food sources should also directly benefit other vertebrates, including deer mice (*Peromyscus* spp.), Townsend's chipmunks (*Tamias townsendii*), and Douglas' squirrels *Tamiasciurus douglasii* (Carey 1995; Carey and Johnson 1995).

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