
Relationships among fungi and small mammals in forested ecosystems

Introduction

Our approach

Here, we will present information about relationships between small mammals and an important food source, fruitbodies of (predominantly) ectomycorrhizal fungi. After providing some background on the function and diversity of the fungi involved, we will examine historical interest in mycophagy and current questions. The main focus will be on mycophagy (fungi consumption) and potential effects of disturbance on the interrelationships among trees, truffles, and mammals. We have not limited our discussion to western North America because much relevant research has occurred in Australia.

Mycorrhizae

Different plants form different types of mycorrhizae with different fungi. The Pinaceae are primarily ectomycorrhizal, the Cupressaceae primarily vesicular-arbuscular (VA) mycorrhizal, as are most herbaceous plants. Some genera or families, such as the Salicaceae, can regularly form both ecto- and VA mycorrhizae. The Ericales mostly have their own distinctive mycorrhizae, as do the orchids. The fungi that form these different mycorrhiza types have different dispersal strategies. Though general categories of mycorrhizae are usually defined in morphological terms with little regard to ecology (Smith and Read 1997) mycorrhizal associations can also be categorized ecologically – such as by the degree of dependence of tree species on mycorrhizae for growth and reproduction. This approach lends itself to inclusion of the spore dispersal mechanisms of the mycobiont in a broader ecological context (Trappe and Luoma 1992).

We will focus on ectomycorrhizal fungi (EMF) because those species seem to be the most important with regard to small mammal mycophagy. Ectomycorrhizal fungi form symbiotic relationships with trees and other vegetation. Trees supply carbon from photosynthesis to the fungi, in turn, EMF absorb water, minerals, and nutrients from the soil and transfer them to tree roots (Smith and Read 1997). Mycorrhizae are essential for the survival and growth of most coniferous forest trees and other shrubs and herbaceous vegetation (Smith and Read 1997).

Douglas-fir (*Pseudotsuga menziesii*) forests have tremendous EMF diversity. For example, across its range, Douglas-fir can form mycorrhizal associations with an estimated 2000 species of fungi (Trappe 1977), yet little data exist on the diversity, abundance, synecology, or autecology of these fungi. Ectomycorrhizal fungus species vary in their fruiting season and abundance (Fogel and Hunt 1979, Fogel 1981, Hunt and Trappe 1987, Luoma 1988, 1991, Luoma et al. 1991, Amaranthus et al. 1994, Luoma et al. 1997, North et al. 1997, States and Gaud 1997, Colgan et al. 1999) and in nutritional value (Fogel and Trappe 1978) as further discussed in a subsequent section of this paper.

Sporocarp production

Factors that influence the fruiting of EMF include rainfall, temperature, and various other abiotic and biotic factors (Fogel 1981, Villeneuve et al. 1991). EMF fruiting is often non-uniform, varying from a few, scattered fruit bodies to concentrated clusters of numerous fruit bodies (Fogel 1976, North et al. 1997, States and Gaud 1997, Waters et al. 1997). The presence and abundance of EMF species may change during forest development (Trappe 1977, Mehus 1986, Termorshuizen 1991). Difficulties with sporocarp sampling methodologies and spatial and temporal variability (Luoma 1991) have hampered efforts to integrate sporocarp biomass data with other forest parameters such as wildlife feeding habits and populations (Cázares et al. 1999).

Fleshy sporocarps that form underground may be broadly referred to as truffles for convenience, though some are Ascomycetes (true truffles), others Basidiomycetes (false truffles), and a few sporocarpic Zygomycetes.

Historical precedents

"... for where the fungus is plentiful there the rats are also plentiful, or it may be the other way round."

H. E. PARKS, 1919.

Thus was one of the most crucial questions currently facing wildlife managers succinctly stated by one of the first naturalists in western North America to document the importance of truffles in the diet of certain small mammals. Harold Parks was an indomitable truffle collector and general observer of nature. During his excursions about the San Francisco Bay area, he noted the strong association between woodrats (*Neotoma* spp.) and these underground fruiting bodies of ectomycorrhizal fungi.

Observations of mammal mycophagy have been recorded since at least the 1800's. Reess and Fisch (1887) addressed the dissemination of spores of *Elaphomyces* (stag truffle) by animals (both wild and experimental) and concluded that spores pass through the animals unchanged. Some of the earlier writings on animal mycophagy included an occasional sighting of mushroom consumption but it was not until Cooke (1890) issued a call for a systematic assessment of this behavior that in-depth observations were initiated.

Hastings and Mottram (1916) took up the call and instigated field studies in Great Britain. Based on their observations, they speculated that succulent mushrooms became very important in the diet of rodents during the late fall and, further, that only in the case of buried sporocarps (truffles and false truffles) "do rodents appear to assist materially the fungus in the distribution of the spores."

Buller (1919, 1922) was inspired by the Hastings and Mottram work and published reports on the mycophagy of the red squirrel (*Tamiasciurus hudsonicus*) in North America. Buller provided reports of bulk storage of mushrooms and of fruitbodies being hung individually in the forks of tree branches. Both methods of caching were common in various parts of the squirrel's range.

Mycophagy of the red squirrel in the extreme western part of its range was investigated by Hardy (1949). He noted that this was near the limit of the dry winter conditions necessary for prolonged preservation of fungi. One cache of fungi was composed of 59 specimens in an excellent state of preservation and occupied a volume of about 4 l. The truffle genus *Hymenogaster* comprised about half of the cache and the mushroom genus *Russula* was the next most common item. He also found lichen in the cache and concluded that lichens formed a portion of the squirrel's diet (Hardy 1949).

Fogel and Trappe (1978) reviewed papers from the intervening years and documented a general trend of mycophagy in the diets of many small mammal species. They also posed several questions relevant to the life histories and ecosystematic roles of fungi and animals. Some of those we will

address here, such as: what food values do mycophagists derive from fungi and what role does mycophagy play in fungus dispersal? Their questions led to much valuable research that provides the foundation for our section on current issues and research. Others of their questions remain in need of investigation.

Web-of-life relationships

Moving beyond simple observations of mycophagy, many important aspects of the interdependencies among fungi, mycophagists, and forest trees have been explored by researchers during the last 20 years. Truffle fungi are primarily dispersed by small mammals that eat the sporocarps and subsequently disperse spore-packed fecal pellets (Fogel and Trappe 1978, Kotter and Farentinos 1984a, Lamont et al. 1985, Maser and Maser 1988a, Claridge et al. 1992). Spores of a few truffle species, particularly in the genus *Elaphomyces*, are also disseminated by air. The edible outer layer of *Elaphomyces* encloses a powdery spore mass that may be discarded while a small mammal is perched above the ground, resulting in the release of spores into the air-stream (Ingold 1973, Trappe and Maser 1977).

Spores can germinate to form new fungal mycelia or fuse with existing fungi, thus colonizing new areas or increasing the genetic diversity of existing fungus populations (Fogel and Trappe 1978, Miller et al. 1994). Forest dwelling small mammal species that depend upon fruiting bodies of EMF contain a diverse array of truffle genera in their fecal material (Maser et al. 1978a, 1985, Colgan et al. 1999, Carey et al. 2001).

As truffles mature, they produce strong, chemically complex odors that attract many small mammals (Trappe and Maser 1977, Donaldson and Stoddart 1994). The scent a truffle exudes may contain chemical compounds similar to certain animal hormones. Human odor trials suggest that males and females may respond to these odors differently (Marin and McDaniel 1987). Responding to these olfactory cues, small mammals are extremely adept at uncovering mature sporocarps (Pyare and Longland 2001a). With consumption of the truffle, many fungal spores are ingested; these spores remain viable after passage through the animal's digestive tract (Trappe and Maser 1976, Kotter and Farentinos 1984b). Some studies suggest that the spores of some truffle species actually require passage through an animal's digestive tract before they will germinate (Lamont et al. 1985, Claridge et al. 1992). Claridge et al. (1992) found that spores obtained directly from sporocarps of the Australian truffle, *Mesophellia*

pachythrix, applied to eucalyptus trees didn't form any ectomycorrhizae whereas *M. pachythrix* spores that came from fecal pellets did. However, they could not determine whether it was passage through the gut or some other factor that allowed the spores to germinate in natural forest soil conditions.

As prey for raptors (e.g., goshawks) and mammalian carnivores (e.g., martens and fishers) small mammals form important links in the trophic structure of forest ecosystems (Fogel and Trappe 1978, McIntire 1984, Hayes et al. 1986, Carey 1991). The potential for indirect consumption of truffles by predators of small mammals has been recognized, but there is also evidence that fishers consume truffles directly (Grenfell and Fassenfest 1979, Zielinski et al. 1999). A wide variety of animals and trophic relationships, then, are instrumental in distributing mycorrhizal fungi to new tree roots. The animals at the same time depend on the trees for cover and reproductive sites (Aubry et al. 2003). Disruption of any part of this inter-dependent web of organisms will inevitably affect the others. Improved understanding of these relationships can lead to improved approaches to management of forest ecosystems (Aramanthus and Luoma 1997, Lawrance 1997, Colgan et al. 1999, Carey 2000, Wilson and Carey 2000, Carey 2001, Carey and Harrington 2001, Carey and Wilson 2001).

Mycophagy

Methods

Animal mycophagy studies are mainly based on stomach content or fecal pellet analyses (Tevis 1953, Fogel and Trappe 1978, Maser et al. 1978a, Maser and Maser 1988a, Carey 1995, Waters and Zabel 1995, Currah et al. 2000). These analyses can provide an accurate record of an animal's recent meals. Fecal samples provide a non-lethal method useful for long-term and integrated studies of diet habits. An effective and widely used method for analyzing fungi in diets was developed by McIntire and Carey (1989). This method utilizes a total of 75 fields-of-view/fecal sample being examined. For each field of view, at 400 × magnification, the presence of each fungal genus and other dietary items is recorded. Colgan et al. (1997) introduced a modification of the method that is useful when a large number of samples needs to be processed and pooling of samples is acceptable under the objectives of the study. When a more detailed assessment of non-fungal components of the diet is needed or if the animal species of interest is thought to be a facultative mycophagist, analysis of gut

contents may be desirable (Currah et al. 2000). Working in western Oregon conifer forests, Carey et al. (1999) determined that the number of animals necessary to sample in order to record all fungal taxa recently consumed by a small mammal population in an area was ≥ 7 .

Identification of the spores found during mycophagy studies has often been problematic due to the lack of comprehensive resources. Castellano et al. (1989) developed a key to spores for truffles of northern temperate forests. That work has now been extensively revised and released in CD-ROM format (Jacobs et al. 2003). In addition to an interactive key, investigators now have access to high-quality illustrations that depict spores and sporocarps of all 98 genera of sequestrate (truffle-like) fungi known from Northern Hemisphere temperate forests.

Case studies

Flying squirrels

Over most of its range, the threatened northern spotted owl feeds primarily on flying squirrels (Forsman et al. 1984, Thomas et al. 1990, Carey 1991) with the exception of the Klamath Province in northern California and southwest Oregon (Zabel et al. 1995). Northern flying squirrels (*Glaucomys sabrinus*), in turn, require truffles as their primary food source (Maser et al. 1985, Hall 1991, Carey 1995, Waters and Zabel 1995, Colgan et al. 1997, Zabel and Waters 1997, Pyare and Longland 2001b). Spring-captured northern flying squirrels from the southern Coast Range of Oregon ate a wider diversity of food items than fall-captured squirrels, though the diet in each season was dominated by fungi (Carey et al. 1999).

Data on stomach contents of northern flying squirrels led McKeever (1960) to conclude that when the snow cover was deep, lichens (also fungal) were the principal food of flying squirrels. With a decrease in snow cover in the spring, the squirrels consumed some truffles. In summer, their entire diet consisted of fungi. In the fall, lichens appeared again but fungi constituted over half the diet. Despite the availability of various seed crops in the three forest types of McKeever's study (*Pinus ponderosa*, *P. contorta*, and mixed *Abies*), no seeds were found in the stomachs. Rosentreter et al. (1997) found a similar seasonal pattern in northern flying squirrel food habits in central Idaho. In contrast, Currah et al. (2000) working in the boreal forest of northeast Alberta, found that flying squirrels consumed substantial amounts of mushrooms and no lichens during the winter. They attributed this result to the ability of flying squirrels to raid the caches of red squirrels.

In one study, the dietary composition of *G. sabrinus* tended to parallel the seasonal availability of sporocarps, suggesting that, in general, it did not prefer particular truffle species under those field conditions (Maser et al. 1986). The notable exception was the consumption of *Rhizopogon* sporocarps, which didn't change with seasonal abundance (Maser et al. 1986). This may have been an artifact of the sample technique or an actual disproportional consumption of *Rhizopogon* by *G. sabrinus*. Subsequent food trial studies under laboratory conditions showed that *G. sabrinus* does have a preference for consuming certain species of truffles over others (Zabel and Waters 1997). Truffles of *Gautieria monticola* and *Alpova trappei* and the lichen *Bryoria fremontii* were the top ranked food items in a comparison of sporocarps, lichen, and seeds. *Rhizopogon* truffles were not included in the experiment, however (Zabel and Waters 1997). Flying squirrels were found to consume significantly more *Gautieria* spores than chipmunks or voles in western Oregon and Washington, though the diets of all three groups were dominated by *Rhizopogon* spores (Jacobs 2002). Since fungal spores may be retained in the gut of flying squirrels for up to 11 days, wide dispersal of spores is possible (Pyare and Longland 2001b).

Knowledge of squirrels' food habits provided insight on a formerly puzzling aspect of northern flying squirrel biology. Bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) prey effectively on flying squirrels, yet to do so they must capture the squirrels on the ground. Biologists had wondered what drew "arboreal" squirrels away from the relative safety of the tree crowns. In this case, of course, they are on the ground to dig out their primary food, truffles (Wells-Gosling and Heaney 1984, Maser et al. 1985).

G. sabrinus utilizes a wide range of forest habitats and has a home range of 3–6 ha (Witt 1992, Martin and Anthony 1999). Thus, management practices that cause local reductions in fungal diversity and abundance may not affect this species as much as species with smaller home ranges. In one study, thinning treatments applied to young stands (35–45 years old) showed no strong effect on *G. sabrinus* density but *G. sabrinus* density was highly positively correlated with truffle biomass and frequency (Gomez et al., unpublished data, in Smith et al. 2003).

Voies

Many small mammal mycophagists eat foods other than fungi, but some have evolved to specialize on hypogeous sporocarps. An excellent example is the western red-backed vole, *Clethrionomys californicus*. Its diet consists largely of truffles supplemented by lichens (Ure and Maser 1982, Hayes

et al. 1986, Maser and Maser 1988b, Thompson 1996, Cázares et al. 1999). The skull and tooth structure of the coastal subspecies (*C. californicus californicus*) are fragile (Grayson et al. 1990) potentially having evolved with a highly specialized diet of soft, hypogeous sporocarps. Its habitat, the coast and Coast Ranges of northwestern California and western Oregon, lies in a relatively rare climate type that permits year-round fruiting of truffles. In the north Coast Range of Oregon, a mean of 85% and up to 98% of the stomach contents of *C. californicus californicus* were truffles (Ure and Maser 1982). Nineteen truffle genera have been identified in the fecal pellets of *C. californicus* in southern Oregon (Hayes et al. 1986). Due to its reliance on a fungal diet, this vole is an important disperser of truffle spores in the forest (Thompson 1996).

Clethrionomys californicus is strongly affected by clear-cutting and forest fragmentation. A strong negative edge effect has been shown both for *C. californicus* population numbers and truffle production, suggesting that truffle distribution in forest remnants may be one of the factors limiting *C. californicus* populations (Mills 1995). *C. californicus* is rarely found in clear-cuts, and intensively logged areas will be nearly devoid of *C. californicus* until the canopy begins to close (Gashwiler 1970, Ure and Maser 1982). As a result, this animal infrequently disperses spores into severely disturbed areas.

In southern New England, Getz (1968) demonstrated that the southern red-backed vole (*C. gapperi*) has high kidney requirements for water and suggested that habitats with "sufficient water or succulent food items" are a necessity for its survival. Truffles, which are high in water content, could potentially fulfill this role.

Although both *C. californicus* and *C. gapperi* are mycophagous, their diets differ according to their habitat. While *C. gapperi* captured in the lowlands of Washington ate as much fungi as *C. californicus* in early fall, *C. gapperi* found in higher elevations in Washington had a much higher incidence of conifer seeds in their stomachs (Ure and Maser 1982). These observations led Ure and Maser (1982) to conclude that mycophagy for these voles is closely related to habitat and not a feature specific to the species. That conclusion was further supported by Maser and Maser (1988b) wherein the stomach contents of *C. californicus* from western Oregon and *C. gapperi* from various areas across North America were examined. They also found that habitat highly influenced the mycophagy of *C. gapperi*, suggesting a facultative aspect to mycophagy in this species. From the Rocky Mountains west, 23 different fungal genera were observed in the diets of *C. gapperi*, but

only seven genera were recorded from animals further east. In comparison, *C. californicus* captured in Oregon consumed 28 fungal genera (Maser and Maser 1988b).

Chipmunks

In contrast to the western red-backed vole and the northern flying squirrel, most small mammals feed not only on truffles (when available) but on a wide variety of other foods (Fogel and Trappe 1978, States and Wettstein 1998, Currah et al. 2000). Townsend's chipmunk, *Tamias townsendi*, eats conifer seeds and has often been regarded as a hindrance to reforestation. However, it avidly eats truffles as well (Tevis 1952, 1956, Maser et al. 1978a, Carey et al. 1999). The Siskiyou chipmunk (*Tamias siskiyou*) is also highly mycophagous. Animals trapped in Jackson County, Oregon had 16 different genera of truffles in their stomach contents, with 96% to 99% of the stomachs examined containing truffle spores (McIntire 1984).

During the early years following clear-cutting, chipmunks transfer mycorrhizal fungal spores from intact forests into timber harvest units. As the vegetation recovers from disturbance, truffles, fruits, seeds, and other foods become available. In times of shortage of other foods, truffles can be critical to chipmunks. As noted by Tevis (1952) only "individuals living where hypogeous fungi flourished became heavy and fat" before hibernation. The chipmunks' propensity for fungi and their movements between forests and timber harvest units make them an important vector of truffle spores (Tevis 1952, Trappe and Maser 1976, Maser et al. 1978a, 1978b, Maser and Maser 1988a, Rosenberg 1990).

Northern and southern hemisphere parallels

The trees, fungi, and mammals of the northern and southern hemisphere have evolved in striking parallelism since their separation by continental drift. This has become evident from research over the past 25 years, especially in North America and Australia. Australia has a higher diversity of species of truffles than is known from anywhere else. Claridge et al. (2000) found over 250 species in an area of southeastern Australia only about 300 km in diameter, more species than are known from all of Europe. The Australian climate, characterized by warm spells and drying winds intervening in the cool, wet times of year when mushrooms fruit, seems to have provided the selection pressure for fungi to evolve to a fruiting habit below ground (Thiers 1984). In the moist coolness of the soil the fungi can

mature their spores regardless of the weather above ground. The success of the hypogeous strategy, however, requires an alternative to the mushroom's discharging of spores using moving air as the agent of dispersal. Mycophagy is one such alternative in Australia, as it is in North America.

In both the northern and southern hemispheres, mammals have evolved or adapted to using hypogeous fungi as an important food source. Some North American rodents such as the northern flying squirrel depend on hypogeous fungi as their major food, whereas others such as deer mice (*Peromyscus* spp.) may eat the fungi opportunistically as a lesser part of their overall diet. In Australia, marsupials vary similarly. The diet of the long-footed potoroo (*Potorous longipes*) is about 90% hypogeous fungi, whereas hypogeous fungi may be only seasonally important in the diet of bandicoots (*Perameles* spp.). Potoroos, bandicoots, bettongs (*Bettongia* spp.), and native Australian rodents such as bush rats (*Rattus fuscipes*) and smoky mice (*Pseudomys fumeus*) are mycophagists analogous to the forest rodents of North America.

Large mammals such as deer (*Odocoileus* spp.), elk (*Cervus elaphus*), mountain goats (*Oreamnos americanus*), and bear (*Ursus* spp.) also feed on hypogeous fungi in North America, providing possibilities for longer dispersal distances than by the small rodents. The Australian equivalents are wallabies (*Wallabia* spp), medium-sized kangaroos that can travel substantial distances in the course of a day. Through examinations of fecal material, Claridge et al. (2001) found that wallabies frequently eat truffles. Scats of numerous larger marsupials such as wombats (*Vombatus* spp.) and gray kangaroos (*Macropus fuliginosus*) were also checked, but none have been found to contain truffle spores.

The interactions of trees, fungi, small mammals, and predators in North America are epitomized in the mature conifer forests of the Pacific northwestern United States. There hypogeous fungi depend on their ectomycorrhizal tree hosts for energy, the northern flying squirrel depends on the fruitbodies as a primary food source, and, at the same time, is the primary prey of the threatened northern spotted owl. Analogous interactions seem likely in Australia (Claridge and May 1994). For example, in mature eucalypt forests hypogeous fungi form ectomycorrhizae; the smoky mouse eats their sporocarps, and the threatened sooty owl (*Tyto tenebricosa*) preys on the mice.

These independently evolved parallels between the northern and southern hemispheres may seem remarkable. However, they simply evidence the success of the hypogeous fungal fruiting habit in conjunction

with mycophagy for increasing fitness of the plants, fungi, and animals participating in the system.

Nutritional value of hypogeous sporocarps

Sporocarps of ectomycorrhizal fungi generally contain much higher concentrations of minerals than do the leaves and fruits of plants. Phosphorus and zinc, for example, are 20 to 50 times more concentrated in sporocarps than in leaves of plants commonly browsed by animals (Stark 1972). Trace elements, too, can be concentrated at relatively high rates in the fungi; for example, copper and selenium. Large animals such as bear, deer, and wallabies may ingest sporocarps more for the mineral content than for other nutritional needs, using the fungi as a type of salt lick (Fogel and Trappe 1978).

The small mammals that depend strongly on hypogeous sporocarps for nourishment, in contrast, appear to do so to meet most of their nutritional needs, and mycophagist specialists such as western red-backed voles, northern flying squirrels, and long-footed potoroos have little else in their diet. Stomach content and fecal analyses reveal that these specialists almost always feed on diverse species in a given day. This is true even of the very small rodents. The typical volume of a single *Rhizopogon* sporocarp, for example, would exceed the stomach capacity of a western red-backed vole, yet those voles invariably have pieces of at least three and sometimes as many as 12 species in their stomachs at any given time. We can infer, then, that this diversity in their diets reflects a nutritional imperative.

As more studies are undertaken, the nutritional value of truffles to mammals is becoming better known. A large portion of a sporocarp is water, suggesting that quantities must be eaten to gain adequate nutrition (Miller and Halls 1969). However, truffles contain substantially higher amounts of nitrogen, phosphorus, potassium, sodium, iron, and aluminum than some epigeous sporocarps (Fogel 1976, Grönwall and Pehrson 1984). Fungi also contain vitamins (Shemakhanova 1967), non-metallic and metallic elements (Stark 1972), steroids, triterpenes, amines, indoles, and phenols (Catalfomo and Trappe 1970) that could potentially benefit mycophagous animals.

The digestibilities of dry matter, nitrogen, cell wall constituents, and energy in two species of truffles, *Elaphomyces granulatus* and *Rhizopogon vinicolor*, have been studied in detail. In a feeding trial, Cork and Kenagy

(1989) fed captive golden-mantled ground squirrels (*Spermophilus saturatus*) the fruit bodies of *Elaphomyces granulatus*, a common truffle. They compared the digestibility of the fungus to the digestibility of the leaves of a variety of plant species eaten naturally by the squirrels, as well as cones, pine nuts, leguminous foliage, and grass. A high-quality food, rodent laboratory chow, was used as a reference diet. Squirrels were offered pre-weighed amounts of the different foods. During the experiment, squirrels maintained or gained body mass on two of the food types, pine nuts and rodent chow. Squirrels consuming a high daily intake of only *Elaphomyces* lost weight. The digestibility of nitrogen and energy from *Elaphomyces* was lower than that recorded for nearly all the other diets. Although chemical analyses revealed that the nitrogen content of fruit bodies was relatively high, 80% of it was bound in totally indigestible spores that the squirrels rarely ate. Of the remaining 20%, only half was present as protein nitrogen. Sources of energy were tied up in complex, relatively indigestible cell-wall tissue.

The digestible energy requirement of the squirrels was also estimated (Cork and Kenagy 1989). The overall digestibility of *E. granulatus* fruit bodies fell just below the critical threshold for the squirrels to maintain energy balance. For these squirrels, with a relatively simple digestive tract, *E. granulatus* was seen as a marginal but important dietary item when no alternative was available. Moreover, the truffles were readily detectable and required minimal processing time prior to consumption, unlike some foods such as seeds from cones. The truffles, therefore, yielded more energy and nutrients in relation to foraging effort. They suggested that if squirrels cannot maintain normal energy balances by eating truffles, then the minor incorporation of less abundant, higher quality foods may be all that is needed to achieve a positive energy balance.

Claridge et al. (1999) conducted feeding experiments in Oregon with captive northern flying squirrels and western red-backed voles. When fed only a single species of truffle (*Rhizopogon vinicolor*) neither of the animals could maintain their weight. The digestibilities of *R. vinicolor* sporocarps were lower than those of other food types eaten by other mammals of similar size. Voles digested the various sporocarp components as well as did the squirrels, even though average vole body mass was six-fold smaller than that of the squirrels. This supports the hypothesis that western red-back voles, like other microtine rodents, have morphological and physiological adaptations of the digestive system to permit greater digestion of fibrous diets than predicted on the basis of body size. Neither of the animals drank

water during the experiments. Fresh truffles are >70% water by weight (Claridge et al. 1999) evidently enough to meet the water requirements of the mycophagists. Nonetheless, individual species of hypogeous fungi appear to be of only moderate nutritional value for many small mammals. Again, this may account for the animal's habit of eating relatively small amounts of several different species within a day, a behavior that may compensate for differences in digestibility and nutritional quality among truffle species.

Little is known about the nutritional value of fungi for other groups of mycophagous mammals. This extends to the terrestrial marsupials of Australia. In Western Australia, Kinnear et al. (1979) assessed the chemical components of fruit bodies of *Mesophellia*, a significant food for the brush-tailed bettong (*Bettongia penicillata*) a member of the rat-kangaroo family. Analyses of the inner core of the truffles (the portion largely consumed by bettongs) indicated a rich source of lipids (around 40% by dry weight) and crude protein levels of 8% to 10%. Although protein levels were high, analyses revealed they were deficient in certain essential amino acids such as lysine. Other amino acids, particularly cysteine and methionine, were present in large quantities. It was suggested that the imbalances in amino acids in fruit bodies could be largely corrected during digestion. Bettongs and other rat-kangaroos (except the musky rat-kangaroo, *Hypsiprymnodon moschatus*) have special adaptations to the gut, including a large saciform forestomach. The hind-gut is reduced to a well-developed, though simple, caecum and proximal colon. The enlarged sacculated foregut is designed to culture anaerobic microbes that ferment food and convert fungal nitrogen to a form more available for the host animal. This process is called pre-gastric fermentation. Hume (1989) suggested that the foregut of rat-kangaroos might serve as a food storage area, an advantage to an animal subject to predation and needing to minimize feeding time.

By monitoring the passage of labeled chemical markers, Frappell and Rose (1986) studied the movement of digesta through the gut of captive long-nosed potoroos (*Potorous tridactylus*). Food particles entered the foregut, remained up to one hour and then passed into the hindgut, where they remained for seven to eight hours before being excreted. Rose and Frappell concluded that fungi entering the foregut were indeed subject to rapid microbial fermentation but that the hindgut was clearly important in the digestion process. Hume et al. (1993) discovered that most material eaten by long-nosed potoroos and rufous bettongs (*Aepyprymus rufescens*)

bypassed the foregut, but that which did not was retained for periods up to four days. Hindgut digestion was also seen by Richardson (1989) in brush-tailed bettongs, although retention time was only a few hours. It seems that the role of the foregut is to help digest fungi while that of the hindgut is to process lower quality food.

Claridge and Cork (1994) provided the first real evidence that fungal fruit bodies were nutritious for rat-kangaroos. In a controlled feeding trial, captive long-nosed potoroos were fed known amounts of fruit-bodies of two species of truffles, *Mesophellia glauca* and *Rhizopogon luteolus*. Chemical analyses revealed that although the nitrogen concentration was high in both fungi, much of it was in non-protein form or associated with cell walls and was thus presumably of low nutritional value or protected from digestive enzymes. The concentration of cell-wall constituents (fiber) was high in both fungi, suggesting low availability of digestible energy. Nonetheless, potoroos lost little weight and digested much of the dry matter, nitrogen, and energy in the pure fungal diets. Consequently, animals maintained positive nitrogen balances and high intakes of digestible and metabolizable energy. Most other mycophagous mammals in Australia lack an enlarged foregut and most food is digested in the hindgut. The lack of this digestive system may help explain why hindgut-fermenters such as rats and bandicoots seldom rely wholly upon fungi but commonly eat other foods such as seeds and invertebrates.

Studying the reproductive energetics of the Tasmanian bettong (*Bettongia gaimardi*) in a eucalypt woodland, Johnson (1994a) found that when production of truffles was highest, the bettongs were almost entirely mycophagous, whereas at times of low fruit body production the bettongs mainly consumed other foods such as leaves and fruits. Body condition of adult bettongs tended to benefit with increasing amounts of fungi in the diet. When production of truffles increased, energy turnover in adult females and growth rates of pouch young increased concomitantly, suggesting that the fungi provided animals with a surplus of energy, perhaps used in lactation. McIlwee and Johnson (1997) used stable isotopes to determine that nearly all nitrogen assimilated into body tissue by northern bettongs (*Bettongia tropica*) was from fungi. In contrast, the sympatric northern brown bandicoot (*Isodon macrourus*) derived much of its nitrogen from invertebrates and practically none from fungi. This finding was mirrored by patterns in the diet of the same animals.

Current issues

Little information is available on the relationship of EMF sporocarp abundance and species composition to the diets and population abundances of small mammals. Small mammal population densities are highly variable across stands and landscapes (Carey et al. 1992, Rosenberg and Anthony 1992, Witt 1992) and the species composition and abundance of mushrooms and truffles may influence the ability of forests to provide habitat for small mammals (Waters and Zabel 1995).

Effects of disturbance

Studies from the Pacific Northwest indicate that forest management activities can reduce EMF and forest regeneration success (Amaranthus and Perry 1987, 1989, Amaranthus et al. 1990). In these studies, the abundance and rapidity of ectomycorrhiza formation was critical to seedling survival and growth, especially on harsh sites. However, across the Pacific Northwest the degrees of reduction of EMF and impacts on forest regeneration vary widely and depend on many factors. Ectomycorrhizal fungus species vary in their abilities to provide particular benefits to their hosts, and presence and abundance of EMF species change during forest succession (Trappe 1977, Mason et al. 1983, Trappe 1987, Visser 1995). The abundance and composition of truffle production may also change following natural disturbance (Luoma 1988, Luoma et al. 1991, Waters et al. 1997).

Many vegetational and structural changes during succession in Douglas-fir forests are documented (Franklin et al. 1981, Spies et al. 1988). Yet, despite the importance of ectomycorrhizal fungi to ecosystem processes, little is known about their community structure and dynamics in managed stands. Such data are essential to predict impacts of disturbance and management on ecosystem productivity. Integration of vegetation, wildlife, and landscape responses with knowledge of EMF and underground functions is needed to elucidate critical aspects of the ecology of EMF that have strong management implications. Only integrated research can provide the extended perspective needed to produce information on interactions among mycorrhizal fungi, small mammals, and a range of forest management practices.

Young managed stands may have a different composition of truffle species than old-growth or natural mature stands. Among *Tsuga heterophylla* dominated forests of varying ages studied across northwest Washington by North et al. (1997) truffle species richness was highest in

the old-growth stands. The standing crop of truffles was much higher in the natural mature and old-growth stands than in the young managed stands. This was largely due to the presence of large clusters of *Elaphomyces granulatus* in the natural stands. A similar trend was found in *Abies amabilis* stands of western Washington. The annual production of truffles was only $1 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ in 23-year-old stands, whereas in the 180-year-old stands, production was $380 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{year}^{-1}$ (Vogt et al. 1981). Stands that had been altered by management prescriptions such as slash burning and soil scarification showed marked reductions in their ability to provide truffles for small mammals when compared to unmanaged stands (North and Greenburg 1998).

Clear-cutting

Ecmycorrhizal fungi and the production of truffles are closely linked to host trees. When the trees are removed or the composition of a stand changes, the composition, species richness, or abundance of truffles in the stand changes as well (Amaranthus et al. 1994, Clarkson and Mills 1994, North et al. 1997, Colgan et al. 1999). Clear-cutting forests is especially detrimental to EMF diversity and abundance because all potential hosts are removed. The removal of the host tree cuts off the supply of carbon to the fungus and prevents it from producing truffles (Amaranthus et al. 1994). Additionally, soil temperature or moisture changes and soil compaction will heavily impact the production of truffles (Fogel 1976, Waters and Zabel 1995, Cázares et al. 1998).

A positive relationship between truffle production and coarse woody debris (CWD) was found by several researchers (Luoma 1988, Amaranthus et al. 1994, Waters et al. 1997). Many forest management practices impact the amount and decay class of CWD in a stand. This too, may affect truffle production, abundance, or diversity. Older forests tend to have more CWD in the later stages of decomposition than do younger or recently clear-cut stands (Harmon et al. 1986). Late-seral forest remnants in southwestern Oregon had 20–40 times more sporocarps than the surrounding 10- to 27-year-old clear-cuts (Clarkson and Mills 1994). Out of the 80 sample plots placed within clear-cuts, only one truffle was found. Within the late-seral stands, truffles were four times more numerous in plots with CWD than without.

When comparing the numbers of truffles and truffle dry weight between Douglas-fir forest fragments and the clear-cuts surrounding them, Amaranthus et al. (1994) also found an association between stand age,

amount of CWD, and truffle production. A greater number, diversity, and total dry weight of truffles were found in the mature stands than in the plantations. Thirteen of the 21 truffle species were found only in the mature stands and eight species were found only under CWD. The effect of CWD upon truffle production was evident only in the mature stands. In the mature forest fragments, there were more truffles and greater truffle biomass in CWD compared to soil (Amaranthus et al. 1994). Since well-decayed CWD retains water, truffle production may be limited to areas in and around well-decayed CWD during times of drought. Retention of mature forest fragments in the managed landscape can help to maintain a diverse food source for small mammals that may not be available in younger stands during critical times (Amaranthus et al. 1994). Though Amaranthus et al. (1994) demonstrated that previously clear-cut young stands produce fewer sporocarps than intact mature forest fragments, only limited information is now becoming available for a range of partial forest harvests and silvicultural systems.

Thinning

Thinning is a common silvicultural practice throughout the world. Unlike clear-cutting, thinning retains residual trees that can act as refuges for EMF. However, thinning still alters the community structure, diversity or composition of EMF in a stand (Waters et al. 1994, Colgan et al. 1999). The effects of variable density thinning (VDT) on truffle production during the first years following thinning was examined by Colgan et al. (1999). Douglas-fir stands were comprised of a mosaic of patches thinned to different densities of standing live trees. The mosaic was divided into two thinning categories, lightly and heavily thinned. Total standing crop truffle biomass was significantly lower in VDT stands compared to control stands. The abundance of *Gautieria* and *Hysterangium* species was lower in thinned stands, while *Melanogaster* species diversity and productivity was highest in VDT stands.

Initial effects of thinning appear to include reduced truffle biomass, reduced frequency of sporocarps, and shifts species dominance (Colgan et al. 1999). Total truffle biomass and frequency of sporocarps may recover 10–17 years after thinning, while shifts in species dominance persist longer (Waters et al. 1994). Potential effects of shifts in truffle species composition include alteration of tree regeneration composition or impacts on mycophagous animals by altering the nutritional balance of their diets.

Green-tree retention

The retention of green trees during commercial timber harvest can moderate the impact of host loss by providing a refuge for EMF diversity. Under the auspices of the Demonstration of Ecosystem Management Options (DEMO) project, Stockdale (2000) examined the initial response of ectomycorrhizae to a 15% basal-area retention treatment. Ectomycorrhizal root tips beneath the crown of retained trees and in open areas away from the retained trees were evaluated. Ectomycorrhizal fungus richness was reduced by as much as 50% in open areas compared to within the dripline of retention trees. Species composition differed between the open areas and within the dripline as well. These results provide evidence that green trees act as refuges for legacy species and are important in maintaining EMF diversity in managed stands. In the longer-term, the DEMO project will be able to examine the role of green-tree retention in the recovery of truffle production after disturbance (Cázares et al. 1999, Luoma and Eberhart 2001).

McIntire (1984) examined the effects of slash burning on mycophagy within a shelterwood-logged coniferous forest in southwest Oregon. The slash treatment was associated with a reduction of spores in fecal samples from Siskiyou chipmunks (*Eutamias siskiyou*) on the site. Waters and Zabel (1995), working in northeastern California, found that heavy logging (shelterwood stands) and intensive site preparation negatively affected flying squirrel populations and truffle frequency.

Disturbance effects on mycophagy and spore dispersal

Many of these studies found a shift in fungal species composition, diversity, and dominance in managed stands. Some also found a difference in biomass and sporocarp frequency between managed and unmanaged stands. Taken as a whole, these studies indicate that forest management practices have a profound effect on EMF communities.

As the diversity, composition, and abundance of truffles in a forest changes, the ability of small mammals to find an adequate amount and diversity of food may be affected. This, in turn, may affect small mammal population numbers or species composition. Pyare and Longland (2001b) suggest that different small mammal species may disperse fungal spores in "ecologically nonredundant ways." Thus, a change in small mammal population composition may reduce dispersal or change dispersal patterns for various fungi.

Evidence also suggests that small mammals of different species compete with each other for the truffle food base (Pyare and Longland 2001b). As truffle abundance is reduced or species become less diverse, those animals heavily reliant upon fungi in their diet may have difficulty finding adequate numbers of truffles. If the small mammal community then changes, predators dependent on small mammals as prey may be impacted (Pyare and Longland 2001b). During periods of low truffle production or when other food sources are not available, the impacts of clear-cutting and thinning on the food supply of small mammals may be more severe (Tevis 1952). These effects may resonate throughout the tightly knit relationship between trees, truffles, small mammals, and predators.

Disturbance down under

Australia has a long history of fire, both wild and deliberately applied, that is thought to have shaped the nature of much of the vegetation and in turn the animals utilizing it. Several studies have focused on the effects of fire on foraging behavior and food resources of rat-kangaroos. In Western Australia, Christensen and Maisey (1987) noted that foraging by brush-tailed bettongs increased dramatically in recently burnt areas, apparently in response to truffle formation. Similarly, in northern Tasmania, Taylor (1992, 1993) compared the foraging activity of Tasmanian bettongs in plots within unburned and recently burned woodland. The density of forage-diggings of animals on burned plots on lateritic soils was tenfold higher than elsewhere across the study area, and this activity began a few days after the fire event. Most forage-diggings in the burned plots had the remains of truffles, entirely from species within the family Mesophelliaceae. Taylor speculated that because of a gap of several days before forage-diggings were made, stimulation of fruiting had actually occurred.

To explain the responses observed by Christensen and Maisey (1987) and Taylor (1992, 1993), Johnson (1994b, 1995) set up a series of experimental burns in a Tasmanian woodland dominated by *Eucalyptus tenuiramus*, which was the preferred habitat of a local population of Tasmanian bettongs. He established a series of matched sites, some subject to deliberately applied (prescribed) fire, the others remaining as unburned or control sites.

In the first set of small-scale fires, Johnson (1994b) found that the density of forage-diggings of bettongs increased three- and ninefold within one month post-fire, then returned to pre-fire levels within four months

and matched forage-digging densities on control sites. A similar result was recorded during the second experiment, with the density of forage-diggings increasing eightfold (Johnson 1995). The relative abundance of fungal fruit bodies changed somewhat, but these changes differed in relation to the intensity of fire. The overall result was that long-term productivity of fungal fruit bodies did not differ significantly across all sites, burned or unburned.

In the second experiment, in which truffles were collected from within exclosures, there were no significant increases in truffles around trees on burned plots (Johnson 1995). Instead, fungal productivity on the burned site remained stable. This contrasted with the unburned control site, where fungal productivity decreased after one month post-fire, but later recovered and surpassed that on the burned site seven to ten months post-fire.

In summary, Johnson (1994b, 1995) concluded that fire had actually triggered the fungi to fruit, but the data indicated that the fungal response was complicated and perhaps unpredictable. Whatever the cause, given that increases in foraging activity occurred mostly within two to three days post-fire, the response was extremely rapid. The ability of kangaroos to rapidly enter burned areas and consume fungi may lead to efficient dispersal of fungal spores that later germinate and form ectomycorrhizal associations on host plant roots. These interactions are critically important to plant recovery post-disturbance in Australia's fire-prone and fire-adapted *Eucalyptus* forests.

More recent experiments by Vernes and Hayden (2001) and Vernes et al. (2001) at Davies Creek in northeastern Queensland largely corroborate the patterns observed by Johnson (1994a, 1994b, 1995) in Tasmania. They found that significantly more animals within the study population chose to forage in burnt habitat than in unburnt habitat. Moreover, they found that foraging success (i.e., probability of recovering a truffle) of animals was higher in burnt than unburnt sites (Vernes and Hayden 2001, Vernes et al. 2001).

The longer-term influences of disturbances on fungal populations are largely undocumented. Johnson (1995) compared diversity and relative abundance of truffles at six sites matched for soil, vegetation, and climate but differing in time since last fire (1, 2, 4, 10, 25, and 50 years). Notably, all fungal taxa present in recently burned sites were also present at sites long unburned. In conclusion, Johnson (1995) suggested that too frequent fire may be detrimental to the fungi and, in turn, animals such

as the Tasmanian bettong, and that intervals around ten years between fires might be optimum. Relationships among time-since-disturbance, litter accumulation, and diversity of ectomycorrhizal mushrooms have been found in other studies (Dighton and Mason 1985, Dighton et al. 1986).

Differences in fungal diversity between sites varying in time since disturbance were also noted by Claridge et al. (1993) in southeastern mainland Australia. There, long-nosed potoroos fed on a higher diversity of fungi in a site never logged than in a site with recent intensive logging. Moreover, the relative abundance of different fungi also varied between the two stands, with the spores of some taxa (Mesophelliaceae) more commonly represented in the scats of animals from the recently logged site than the site never logged. Recent studies by Green and Mitchell (1997) of the long-footed potoroo, an obligate fungivore, suggest that animals in sites with minimal recent disturbance may have higher fecundity, and forage for significantly shorter periods, than animals in habitats with evidence of recent disturbance.

Potoroos, in contrast to bettongs, prefer dense understory vegetation. The long-footed potoroo and long-nosed potoroo also apparently benefit from lack of recent disturbance to their habitats. Recent work by Claridge and Barry (2000) in southeastern mainland Australia showed that the probability of occurrence of detecting forage-diggings of these animals was higher in sites burned more than 20 years previously, compared to sites burned 0–10 and 11–20 years previously.

Summary

Truffle fungi are primarily disseminated by small mammals that eat the sporocarps and subsequently disperse spore-packed fecal pellets. The spores can germinate to form new fungal mycelia or fuse with existing fungi, thus colonizing new areas or increasing the genetic diversity of existing fungal populations. Although small mammals consume both mushrooms and truffles, forest-dwelling mycophagists in western North America predominantly utilize a diverse array of truffle genera in their diets.

Animal mycophagy studies are mainly based on stomach content or fecal pellet analyses. These analyses can provide an accurate record of an animal's recent meals. Fecal samples provide a non-lethal method useful for long-term and integrated studies of diet habits. Assessment of the

relative frequency of spore types and other dietary items is commonly used to rank the importance of food items. Truffle spores remain viable after passage through the animal's digestive tract. The spores of some truffle species require passage through an animal's digestive tract to improve germination.

The trees, fungi, and mammals of the northern and southern hemisphere have evolved in striking ecological parallelism since their separation by continental drift. Truffles are abundant in Australian *Eucalyptus* forests, as are mycophagous marsupials. The effects of fire on truffle production and mycophagy have been more extensively investigated in Australia than in North America. Consumption of truffles in the family Mesophelliaceae increased after fire and five alternative hypotheses were proposed to account for the phenomenon. First, fire may remove ground cover, thereby improving access to the soil and hence truffle resources. Second, animals may dig more often for fungi in recently burned habitats because other foods become unavailable. Third, fire may actually stimulate the truffles to form. And fourth, heating of existing truffles may change their odor such that they become more detectable.

Knowledge of the nutritional value of truffles to mammals is increasing. A large portion of a sporocarp is water, suggesting that quantities must be eaten to gain adequate nutrition. The digestibilities of dry matter, nitrogen, cell-wall constituents, and energy suggest that, as single species, truffles are of moderate nutritional value. Tests of multiple-species diets have not been published. Small mammals that depend strongly on truffles for nourishment appear to use a diversity of species to meet their nutritional needs. The anatomy of the digestive system may influence the degree to which small mammals can rely on fungi as a food source.

As the diversity, composition, and abundance of truffles in a forest changes, the ability of small mammals to find an adequate amount and diversity of food may be affected. This, in turn, may affect small mammal population numbers or species composition. Alternatives to clear-cutting may mitigate the loss of EMF in managed forest ecosystems. Various squirrels, chipmunks, and voles are ecologically important mycophagists that disperse truffles in forested habitats, contribute to the recovery of truffle species in second-growth stands, and provide part of the prey base for a variety of predators. Increased consideration of these ecological relationships and functions will aid in achieving ecosystem management objectives.

Research needs

Questions relevant to small mammal mycophagy in western coniferous forests abound. The fundamental dilemma posed by Parks (1919) has yet to be fully addressed: to what extent are small mammals dependent on truffles (and hence occur at greater densities in truffle-rich habitats) and to what extent do truffle-producing EMF species depend on small mammals for spore dispersal and dominance in the fungal community (and hence attain high levels of sporocarp production)? The nutritional value of a wide variety of truffle species needs to be determined. Ecosystem responses to disturbance are important concerns. What is the rate of re-establishment of these linked ecosystem components (small mammals and truffles) following disturbance? Studies of the role of fire are particularly needed in western coniferous ecosystems. Experimental research will be necessary to test the applicability of conclusions and hypotheses generated by research in Australian fire-adapted ecosystems. What are the processes that facilitate re-establishment of truffles and small mammals in a disturbed ecosystem? What are the functions of coarse woody debris in these processes? What can managers do to maintain fungal resources in ecosystems and how can recovery from disturbance be facilitated?

Whatever questions researchers choose to pursue, broad, important, commonalities can be fostered. Interdisciplinary experiments with long-term objectives and stable funding sources should be emphasized. Integration of stand-level studies with landscape research is desirable. Iterative rounds of data acquisition and modeling will be necessary to advance ecosystem-science-based forest management.

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