Folia Biologica et Oecologica 10: 89–95 (2014)
Acta Universitatis Lodziensis

DE GRUYTER OPEN

Small mammals feeding on hypogeous fungi

MAŁGORZATA POŁATYŃSKA

Department of Algology and Mycology, Faculty of Biology and Environmental Protection, University of Lodz, Banacha 12/16 90-237, Lodz
E-mail: mpola@biol.uni.lodz.pl

ABSTRACT

Fungi serve as a food source for a wide variety of animals. Among mammals, most species feed on fungi occasionally or accidentally while foraging for other type of food, but some species are frequent mycophags and fungi can be a dominant component of their diet. Examples of mycophags can be found among marsupials: wallabies and bettongs; and rodents: squirrels, chipmunks, voles and mice.

Hypogeous fungi produce closed, underground sporocarps without opening mechanisms, and thus are unable to release their spores into the air. In case of those fungi, animals feeding on sporocarps and spreading spores in their faeces are considered to be the main vector of spore dispersal. Animals that frequently feed on fungi and other heavy digestible food have developed morphological adaptations such as longer gut retention and a spiral construction of the proximal colon, to digest more fungal material which is rich in nitrogen.

The spores stay viable after passing through the animal gut, and in some cases their ability to germinate and form mycorrhiza is enhanced after leaving the intestine. Hypogeous fungi are mycorrhizal partners for plants and it is therefore possible that the interactions between mycorrhizal fungi and animals spreading their spores also play an important role in ecosystem functioning.

KEY WORDS: mycophagy, fungivory, spore dispersal rodents

Introduction

Mycophagy, or fungivory is a feeding habit of consuming fungi. Depending on the degree to which animals feed on fungi, mycophagy can be: obligatory – the diet consists entirely or mostly of fungi; preferential – fungi are preferred to other food types but the animal feeds regularly on different food sources; opportunistic – fungi are eaten occasionally and accidental when fungi are eaten while foraging for a different kind of food (Trappe *et al*. 2009).

DOI: 10.2478/fobio-2014-0006

Fungivory is very common and is mostly associated with snails and insect larvae feeding on "grubby" fruit bodies (Trappe *et al*. 2009), but many groups of vertebrates, like mammals, also make use of this food source. Examples of mammal mycophags can be found in the families of Sciuridae (squirrels and chipmunks), Cricetidae (voles), Muridae (mice), Macropodidae (kangaroos and wallabies), Potoroidae (rat-kangaroos and bettongs), and bigger animals, like Suidae (pigs) and Cervidae (deer) (Fogel & Trappe 1978). Insectivorous mammals, such as shrews (Soricidae), are examples of accidental or opportunistic mycophags that feed on hypogeous fungi while foraging for invertebrates (Kataržyte & Kutorga 2011). Recently primates are becoming a new and interesting group in studies on mycophagy. Mushrooms are not a common food source for those mammals and they mostly enrich the animals' diet, when available. Some examples of primate mycophagy can be observed among macaques, marmosets and lemurs (Hanson *et al*. 2003, Hilario & Ferrari 2011).

As animals can eat the whole fruit body, traces of animal foraging may be difficult to observe and track with the naked eye. Therefore, the prime method for determining whether mammals feed on fungi is microscopic and DNA analysis of faecal samples and intestine contents, for presence of spores. The fungal material can even be found in samples from stomachs and faeces of predatory mammals, since they feed on mycophagous animals (Fogel & Trappe 1978, Lehmkuhl *et al*. 2004).

The aim of this paper is to show some aspects of mammalian mycophagy regarding feeding on a particular food source that are hypogeous fungi. The case studies presented here will consider two mammal groups: rodents (Rodentia) and marsupials (Marsupialia), having well known records of mycophagy and hereafter referred as small mammals.

Hypogeous fungi as a food source

Macroscopic fungi produce fruit bodies on the ground to enable spore dispersal which is additionally enhanced by releasing mechanisms. This, however, does not occur in hypogeous fungi. These fungi produce closed, underground sporocarps with no opening mechanisms. As the spores cannot be released into the air, the main way for their dispersion is through animal activity (Johnson 1996). Animals take part in spore dispersion in a couple of ways: by digging up, and thus opening the sporocarps and releasing spores into the air, by eating the sporocarps and spreading spores in faeces or by carrying spores on their bodies after walking through an already decayed sporocarp (Cork & Kenagy 1989, Johnson 1996, Trappe *et al*. 2009). Some hypogenous fungi produce sporocarps in more than one season of the year. For example, *Elaphomyces,* which is the most common genus of truffle-like fungi in Poland, produces fruit bodies in the spring, summer and autumn, and usually more than one generation of fruit bodies can be found (immature, mature and overriped). In humid periods, old fruit bodies break up, producing an intense smell (Ławrynowicz *et al*. 2006). The mature fruit bodies produce characteristic aromas resembling hormones attracting animals. The chemistry of those odours and animal reaction to them differ among species (Fogel & Trappe 1978, Johnson 1996, Trappe & Claridge 2005). Chemical analyses suggest that the major compound responsible for the characteristic smell of truffles is dimethyl sulphide. An earlier hypothesis that those aromas resemble pheromones was rejected experimentally using dogs and pigs (Johnson 1996).

Fungal cell walls are built of carbohydrates, primarily of chitin, which can be digested only by some animals (Cork & Kenagy 1989, Claridge *et al.* 1999). For those who can digest them, hypogeous fungi are a source of phosphorus, potassium, calcium, magnesium, and most important – nitrogen (Johnson 1996, Claridge *et al.* 1999, Trappe *et al.* 2009). 80% of the nitrogen is contained in the indigestible spores, and from the remaining 20%, only a half is in the form of proteins, and the other half is built into complex and mostly indigestible structures of cell walls (Cork & Kenagy 1989, Johnson 1996, Claridge *et al.* 1999, D'Alva 2007, Trappe *et al.* 2009).

Fungi are also a source of water, which constitutes 80-90% of their mass (Claridge *et al.* 1999, Trappe *et al.* 2009). It is possible that the high concentration of water in hypogeous fungi, and their relatively low dry mass makes them nutritious, when eaten in large numbers. Therefore, in the autumn, when hypogeous fungi appear in abundance, the cost of foraging for this type of food is lower than for other food sources. Moreover, animals can easily find intensively smelling matured fruit bodies, and along with them, a concentration of more fruit bodies than they can consume in one intake (Cork & Kenagy 1989, Johnson 1996). In the case of small mammals, the balance of costs and benefits from foraging for fungi is little above zero. As a result, although this is enough for them, it is not enough for larger mammals, like deer, which in turn eat fungi less frequently (Fogel & Trappe 1978, Cork & Kenagy 1989, Trappe *et al.* 2009).

The spores of hypogeous fungi pass through an animal's digestive system with no changes in their structure and stay viable after leaving it (Cork & Kenagy 1989, Claridge & Lindenmayer 1998, Claridge *et al.* 1999, Trappe *et al.* 2009). While inside the alimentary canal, spores are subject to heat and chemical treatment, of which both can stimulate spore germination. However, the mechanism of these factors' influence on the spores remains unclear and the evidence is mixed. The laboratory studies by Colgan and Claridge (2002) support the hypothesis that the passing of spores through an animal's digestive system can enhance the spores' ability to germinate, but it differs depending on the mycophagous animal species. This is due to the differences in mycophags gut retention, body temperature and digestive system structure (Colgan & Claridge 2002). Another factor are the conditions required for germination, which also differ among fungal species (Trappe & Claridge 2005).

Examples of small mammal mycophagy on hypogeous fungi

Small mammals usually eat fungi as a part of a diverse diet that includes fruit, seeds, herbs, invertebrates and other food sources but they may, in some cases, prefer fungi to other food items (Fogel & Trappe 1978, Johnson 1996, D'Alva 2007). Examples of mycophagous species along with the dietary volume of consumed fungal material are shown in table 1. The volume for *Bettongia gaimardi* is cited after Johnson (1996), and the other species are cited after Fogel and Trappe (1978) with data taken from works of Trevis (1953), Mckeever (1964), Steinecker and Browning (1970), and Drożdż (1966).

Table 1. The annual dietary volume of consumed fungal material.

	Species	Volume (%)
Marsupialia, Potoroidae	*Bettongia gaimardi*, Tasmanian bettong	90
Rodentia, Sciurudae	*Sciurus griseus,* Western gray squirrel	52
	Spermophilus lateralis, Golden mantled ground squirrel	61
	Tamias amoenus, Yellow-pine chipmunk	37
	Tamias quadrimaculatus, Long-eared chipmunk	66
	Tamias speciosus, Lodgepole chipmunk	32
	Tamias townsendii, Townsend's chipmunk	72
	Tamiasciurus douglasii, Douglas's squirrel	56
Rodentia, Cricetidae	*Myodes glareolus,* Bank vole	7
Rodentia, Muridae	*Apodemus flavicollis,* Yellow-necked mouse	1

Hypogeous fungi serve as a food source for various species of small mammals characterised by different foraging behaviour (Fogel & Trappe 1978, Trappe *et al*. 2009). Australian wallabies, for example, find fruit bodies a couple of centimetres below soil surface, whereas bettongs, which are equipped with longer claws, can dig to the lower parts of the ground profile, thus making their diet more diverse (Verns & Lebel 2011). Australian mammals that feed on fungi are mostly small, eat less plants and their digestive system is adapted for longer gut retention times and fermentation to assimilate more nutrients from heavy digestible fungi (Danks 2012). Some rodents, like voles, have similar adaptations. They are able to digest complex polysaccharides, like chitin, which indicates a complicated fermentation process in the digestive system. Voles are also very effective in reducing losses of nitrogen in faeces, due to the colonic separation mechanism, and a characteristic spiral construction of the proximal colon. This enables them to digest fungal material sufficiently. Some species of voles, like bank vole *Myodes glareolus* and field vole *Microtus agrarius*, practice coprophagy (consumption of faeces) which is also an adaptation for digesting heavy food, particularly cellulose (Cork & Kenagy 1989, Lee & Houston 1993, Claridge *et al*. 1999).

Many squirrels feed frequently on hypogeous fungi, among them the American red squirrel *Tamiasciurus hudsonicus*, Townsend's chipmunk *Tamias townsendii* and northern flying squirrel *Glaucomys sabrinus* (Colgan & Claridge 2002, Bertolino *et al*. 2004). Studies on *G. sabrinus* show that it prefers hypogeous fungi in its diet and consumes them when available. Flying squirrels actively search for fungi on the ground, despite the higher risk of predation from lynxes and coyotes (Trappe *et al*. 2009).

Kataržyte and Kutorga (2011) observed that the *Apodemus* mice, and the bank vole *Myodes glareolus* feed on fungi for most of the year with the number of faecal samples containing spores increasing from 50% in the spring to 83% in the autumn. The number of fungal species found also increased. The most frequently observed genus was *Elaphomyces*. Studying the faecal samples from small mammals in search for spores can be helpful in evaluating the biodiversity of hypogeous fungi on given terrain. Kataržyte and Kutorga (2011) found 9 species of hypogeous fungi in samples from mice *Apodemus sp.*, bank vole *Myodes glareolus*, common shrew *Sorex araneus* and pygmy shrew *S. minutus*, while only 5 species were found during the search for fruit bodies. Moreover, the presence of *Chamonixia caespitosa*, and fungi of the genus *Genea* in Lithuania are documented only from faecal samples from small mammals (Kataržyte & Kutorga 2011).

Relationships in ecosystems – mycophagy and mycorhiza

In comparison with anemochoric spores, zoochoric spores have a significantly larger range of dispersion because foraging areas of small mammals can range from 1 to even 100 ha (Johnson 1996). Studies on population structure of hypogeous fungi show little genetic diversity between neighbouring sites, which means that long distance spore spreading prevents losses in the genetic pool of the population (Johnson 1996, Bertolino *et al*. 2004). Animals carry spores into early successional habitats, like glacier forefronts and burnt down forest patches, where the fungi have fewer competitors (Cazares & Trappe 1994). Additionally, less frequent species of fungi are prevented from competitive exclusion by more widespread species because animals feed on a variety of species and spread spores equally (Johnson 1996).

Hypogeous fungi occupy a very specific niche, being mycorrhizal partners for roots of vascular plants (Fogel & Trappe 1978, D'Alva *et al*. 2007, Trappe *et al*. 2009). They have a positive effect on their host plants, and may also influence the plant community structure in the given area as well as the overall condition of the ecosystem. The interactions between mycorrhizal fungi, their tree hosts and spore dispersing mycophags are the topic of multiple studies conducted in various regions in Europe, North and South America and Australia (Claridge *et al*. 1999). Experimental works have shown that some fungi that originated from spores that passed through animals' digestive systems form mycorrhiza with seedlings more rapidly than fungi from spores that were deposited into soil directly from the fruit body (Johnson 1996, Claridge *et al*. 1999, Colgan & Claridge 2002).

Many animals, both mycophages and predators, depend on trees for shelter, food and breeding places. In turn, the growth of trees is aided by mycorrhizal fungi. Therefore, mycorrhiza and mycophagy may be inseparable phenomena influencing the structure, functioning and stability of the forest ecosystem (Johnson 1996). Any disturbance in this complex net of relations can influence all its other parts. It is vital to expand the knowledge of the forest ecosystem and the interactions between organisms composing it, as it would give us a wider perspective regarding the forest management (Colgan *et al*. 1999).

References

Bertolino, S., Vizzini, A., Wauters, L.A. & Tosi, G. 2004. Consumption of hypogeous and epigeous fungi by the red squirrel (*Sciurus vulgaris*) in subalpine conifer forests. Forest Ecology and Management, 202: 227–233.

Cazares, E. & Trappe, J.M. 1994. Spore dispersal of ectomycorrhizal fungi on a glacier forefront by mammal mycophagy, Mycologia, 86: 507–510.

Claridge, A.W. & Lindenmayer, D.B. 1998. Consumption of hypogeous fungi by the mountain brushtail possum (*Trichosurus caninus*) in eastern Australia. Mycological Research, 102: 269–272.

Claridge, A.W., Trappe, J.M., Cork, S.J. & Claridge, D.L. 1999. Mycophagy by small mammals in the coniferous forests of North America: nutritional value of sporocarps of *Rhizopogon vinicolor*, a common hypogeous fungus. Journal of Comparative Physiology B, 169: 172–178.

Colgan, W., Carey, A.B., Trappe, J.M., Molina, R. & Thyssel, D. 1999. Diversity and productivity of hypogeous fungal sporocarps in a variably thinned Douglas-fir forest. Canadian Journal of Forest Research, 29: 1259–1268.

Colgan, W. & Claridge, W. 2002. Mycorrhizal effectiveness of *Rhizopogon* spores recovered from faecal pellets of small forest-dwelling mammals. Mycological Reseach, 106: 314–320.

Cork, S.J. & Kenagy, G.J. 1989. Nutritional value of hypogeous fungus for as forest-dwelling ground squirrel. Ecology, 70(3): 577–586.

D'Alva, T., Lara, C., Estrada-Torres, A. & Castillo-Guevara, C. 2007. Digestive responses of two omnivorous rodents (*Peromyscus maniculatus* and *P. alstoni*) feeding on epigeous fungus (*Russula occidentalis*). Journal of Comparative Physiology B, 177: 707–712.

Danks, M.A. 2012. Gut-retention time in mycophagous mammals: a review and a study of truffle-like fungal spore retention in the swam wallaby. Fungal Ecology, 5: 200–210.

Drożdż, A. 1966. Food habits and food supply of rodents in the beech forest, Acta Theriologica, 11: 363–384.

Fogel, R. & Trappe, J. 1978. Fungus consumption (Mycophagy) by small animals. Northwest Science, 52(1): 1–31.

Hanson, A.M., Hodge, K.T. & Porter, L.M. 2003. Mycophagy among Primates. Mycologist, 17(1): 6–10.

Hilario, R.R. & Ferrari, S.F. 2011. Why feed on fungi? The nutritional content of sporocarps consumed by buffy-headed marmosets, *Callithrix flaviceps* (Pimates: Callithrichidae), in Southeastern Brazil. Journal of Chemical Ecology, 37:145–149.

Johnson, C.N. 1996. Interactions between mammals and ectomycorrhizal fungi. Tree, 11(12): 503–507.

Katarżyte, M. & Kutorga, E. 2011. Small mammal mycophagy in hermiboreal forest communities of Lithuania. Central European Journal of Biology, 6(3): 446–456.

Lee, W.B. & Houston, D.C. 1993. The role of coprophagy in digestion in voles (*Microtus agrestis* and *Clethrionomys glareolus*). Functional Ecology, 7: 427–432.

Lehmkuhl, J.F., Gould, L.E., Cazares, E. & Hosford, D.R. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management, 200: 49–65.

Ławrynowicz, M., Faliński, J.B. & Bober, J. 2006. Interactions among hypogeous fungi and wild boars in the subcontinental pine forest. Biodiversity: Research and Conservation, 1–2: 102–106.

Mckeever, S. 1964, Food habits of the pine squirrel in northeastern California Journal of Wildlife Management, 28: 402–403.

Steinecker, W. & Browning, B.M., 1970. Food habits of the western gray squirrel. California Fish and Game 56:36–48.

Trappe, J.M. & Claridge, A.W. 2005. Hypogeous fungi: evolution of reproductive and dispersal strategies through interactions with animals and mycorrhizal plants. (In:) J. Dighton, J.F. White & Oudemans P. (eds), The Fungal Community. CRC, Taylor & Francis, Boca Raton, pp. 613–623.

Trappe, J.M., Molina, R., Louma, D.L., Cazares, E., Pilz, D., Smith, J.E., Castellano, M.A., Miller, S.L. & Trappe, M.J. 2009. Diversity, ecology and conservation of truffle fungi in forests of the Pacific Northwest – small mammal mycophagy. United States, Portland, Oregon, Department of Agriculture, 196.

Trevis, L. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. Journal of Mammalogy, 34:316–324.

Vernes, K. & Lebel, T. 2011. Truffle consumption by New Guinea forest wallabies. Fungal Ecology, 4: 270–276.

Streszczenie

Grzyby stanowią pokarm dla wielu gatunków zwierząt. Spośród ssaków, większość gatunków żywi się grzybami w niewielkiej ilości oraz natrafiając na nie w czasie poszukiwania innego pokarmu, jednak dla niektórych gatunków, grzyby mogą stanowić dominujący element diety. Najwięcej przykładów mykofagicznych ssaków można znaleźć wśród małych zwierząt: torbaczy (walabie i kanguroszczury) oraz gryzoni (wiewiórki, myszy i nornice) (Trappe *et al*. 2009).

Grzyby podziemne zajmują bardzo specyficzną niszę ekologiczną, jako partnerzy mykoryzowi drzew, tworzący zamknięte owocniki, nie przystosowane do dyspersji zarodników z prądami powietrza. Z tego powodu głównymi wektorami rozpraszania tych grzybów są zwierzęta odżywiające się podziemnymi owocnikami i roznoszące zarodniki w odchodach. Zwierzęta które regularnie żywią się grzybami posiadają fizjologiczne i morfologiczne adaptacje do trawienia tego typu pokarmu i uzyskania z niego jak największej ilości przyswajalnej materii. Zarodniki pozostają zdolne do dalszego rozwoju po wydaleniu na zewnątrz organizmu zwierzęcego. Badania laboratoryjne wskazują, że w przypadku niektórych gatunków wpływa to wręcz korzystnie na tempo dalszego rozwoju zarodników, oraz na ich zdolność do zawiązywania mykoryzy.

Zwierzęta w ekosystemie leśnym zależą od drzew jako od miejsc schronienia, żerowania i rozmnażania. Tyczy się to zarówno gatunków mykofagicznych, roznoszących zarodniki grzybów podziemnych, jak i zwierząt drapieżnych. Z kolei drzewa zależą od grzybów mykoryzowych wpływających na ich rozwój i kondycję. Ważnym jest zatem, aby poszerzać wiedzę o powiązaniach między organizmami tworzącymi ekosystem leśny, gdyż jakiekolwiek zaburzenie w tej sieci zależności (jak na przykład selektywna wycinka drzew, lub ograniczanie populacji gryzoni uznanych za szkodniki), może wpłynąć na pozostałe elementy ekosystemu (Colgan *et al*. 1999).