# Chapter 21
# Truffles and Small Mammals

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## 21.1 Introduction

Truffles completely depend on mycophagist animals for spore dispersal because they have lost the ability to forcefully eject their spores. Among mycophagist animals, small mammals are the most important (Trappe et al. 2009).

Small mammals feeding on true truffles (*Tuber* spp.) are as diverse as the habitats where truffles grow—from rangelands to thermophilic oak forests and from conifer mountain forest to alpine tundra (references in Table 21.1). They are different in terms of evolutionary history, habitat use, foraging behaviour, dietary preferences and digestive physiology. Most mammal species considered as obligate or preferential mycophagists are small; their body mass is typically about or (much) less than 1 kg (Johnson 1996; Claridge and Trappe 2005; Maser et al. 2008).

The identification of fungi consumed by mycophagists is facilitated by characteristic microscopic features of the spores of hypogeous fungi, which can be found abundantly in gut contents and fecal pellets of small mammal mycophagists. However, in microscopy-based studies, taxonomic resolution is typically limited at the level of genera or species groups (Table 21.1). By isolation of DNA from spores contained in fecal pellets (Schickmann et al. 2011) and by application of metabarcoding technologies, these limitations will be overcome, as soon as reliable reference sequences of hypogeous fungal species from diverse genera and regions will be available.

In this chapter the diversity of small mammals feeding on true truffles and their potential adaptations and specific capacities linked to mycophagy are discussed.

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**Table 21.1** Small mammal species reported to feed on true truffles

| Taxon | Common name | Distribution | Category | References |
|---|---|---|---|---|
| Insectivora, Soricidae, Soricinae | | | | |
| *Sorex araneus* | Common shrew | W-Eurasia | Opportunistic | Schickmann et al. (2012) |
| *Sorex minutus* | Eurasian pigmy shrew | W-Eurasia | Opportunistic | Katažytė and Kutorga (2011), Schickmann et al. (2012) |
| Lagomorpha, Leporidae, Leporinae | | | | |
| *Lepus californicus* | Black-tailed jackrabbit | N-Am | Opportunistic?* | Maser et al. (1988) |
| *Lepus townsendii* | White-tailed jackrabbit | N-Am | Opportunistic?* | Maser et al. (1988) |
| *Sylvilagus nuttallii* | Mountain cottontail | N-Am | Opportunistic | Maser et al. (1988) |
| Lagomorpha, Ochotonidae, Ochotoninae | | | | |
| *Ochotona princeps* | Pika or rock rabbit | N-Am | Opportunistic | Cázares and Trappe (1994) |
| Rodentia, Cricetidae, Arvicolinae | | | | |
| *Microtus agrestis* | Field vole | Eurasia | Opportunistic | Schickmann et al. (2012) |
| *Microtus californicus* | California vole | N-Am | Preferential/obligate | Frank et al. (2008) |
| *Myodes californicus californicus* | Western red-backed vole | N-Am | Obligate | Maser and Maser (1988) |
| *Myodes californicus mazama* | Mazama red-backed vole | N-Am | Preferential | Maser and Maser (1988) |
| *Myodes californicus/gapperi* | Red-backed voles | N-Am | Preferential | Jacobs and Luoma (2008) |
| *Myodes gapperi* | Southern red-backed vole | N-Am | Preferential | Maser and Maser (1988), Pastor et al. (1996), Terwilliger and Pastor (1999) |
| *Myodes glareolus* | Bank vole | W-Eurasia | Preferential | Dróżdż (1966), Katažytė and Kutorga (2011), Schickmann et al. (2012) |

(continued)

**Table 21.1** (continued)

| Taxon | Common name | Distribution | Category | References |
|---|---|---|---|---|
| Rodentia, Cricetidae, Neotominae | | | | |
| *Neotoma fuscipes* | Dusky-footed woodrat | N-Am | Opportunistic | Linsdale and Tevis (1951), Fogel and Trappe (1978) |
| *Peromyscus leucopus* | White-footed mouse | N-Am | Opportunistic | Maser and Maser (1987), Frank et al. (2008), Sidlar (2012) |
| *Peromyscus maniculatus* | Deer mouse | N-Am | Opportunistic | Maser and Maser (1987) |
| *Peromyscus truei* | Pinyon mouse | N-Am | Opportunistic | Maser and Maser (1987) |
| *Reithrodontomys megalotis* | Western harvest mouse | N-Am | Opportunistic?* | Frank et al. (2008) |
| Rodentia, Geomyidae, Geomyinae | | | | |
| *Thomomys bottae* | Botta's pocket gopher | N-Am | Opportunistic?* | Taylor et al. (2009) |
| Rodentia, Gliridae, Glirinae | | | | |
| *Glis glis* | Fat dormouse | Europe, W-Asia | Opportunistic | Schickmann et al. (2012) |
| Rodentia, Muridae, Murinae | | | | |
| *Apodemus flavicollis* | Yellow-necked mouse | Europe, W-Asia | Opportunistic | Schickmann et al. (2012) |
| Rodentia, Sciuridae, Sciurinae | | | | |
| *Glaucomys sabrinus* | Northern flying squirrel | N-Am | Preferential | Carey (1995), Rosentreter et al. (1997), Currah et al. (2000), Lehmkuhl et al. (2004), Gomez et al. (2005), Jacobs and Luoma (2008) |
| *Sciurus aberti* | Tassel-eared squirrel | N-Am | Preferential | Kotter and Farentinos (1984), Dodd et al. (2003) |
| *Sciurus griseus* | Western gray squirrel | N-Am | Preferential | Maser et al. (1988) |

(continued)

**Table 21.1** (continued)

| Taxon | Common name | Distribution | Category | References |
|---|---|---|---|---|
| *Sciurus vulgaris* | Red squirrel | Europe | Preferential?* | unpubl. observation, Brive, SW France |
| *Tamiasciurus hudsonicus* | Red squirrel | N-Am | Preferential | Currah et al. (2000), Vernes et al. (2004), Sidlar (2012) |
| Rodentia, Sciuridae, Xerinae | | | | |
| *Callospermophilus lateralis* | Golden-mantled ground squirrel | N-Am | Preferential | Maser et al. (1988) |
| *Marmota caligata* | Hoary marmot | N-Am | Opportunistic | Cázares and Trappe (1994) |
| *Neotamias amoenus* | Yellow-pine chipmunk | N-Am | Preferential | Sidlar (2012) |
| *Neotamias siskiyou* | Siskiyou chipmunk | N-Am | Preferential | Kotter and Farentinos (1984) |
| *Neotamias townsendii* | Townsend chipmunk | N-Am | Preferential | Maser et al. (1988), Jacobs and Luoma (2008) |

Category of mycophagy (occasional, preferential, obligate) according to Claridge and Trappe (2005), Trappe et al. (2009) and Schickmann et al. (2012) or proposed here (*)
N-Am = North America

The nutritional qualities of true truffles are also summarized and confronted with digestive capacities and food preferences of small mammals.

## 21.2 Diversity of Small Mammals Feeding on True Truffles

Small mammal mycophagy of true truffles is present in various families of rodents; few reports are available for insectivores and lagomorphs. These orders are present across continents in the northern hemisphere. Small mammal species and genera differ considerably between the Palearctic and Nearctic regions (Wallace 1894).

The rodents comprise the majority of species reported to feed on truffles, including many preferential mycophagists. In the partly arboricolous voles of the genus *Myodes* (Cricetidae-Arvicolinae), mycophagy is of particular importance, in both North America (N-Am) and Europe. Three species (*M. californicus*, *M. gapperi*, *M. glareolus*) are considered as preferential mycophagists, *M. californicus* subsp. *californicus* even as obligately mycophagous (Maser and Maser 1988; Trappe et al. 2009). There is important variation in the degree of mycophagy in *Myodes* spp. across habitats, latitudes and altitudes, at the population level and at the subspecies level, in Europe and in N-Am (Hansson 1985; Maser and

Maser 1988), depending on the locally available choice of feed. *Myodes californicus* subsp. *californicus*, which inhabits conifer forests in the Coastal Ranges of Northern California and Western Oregon, was found more strictly mycophagous than subsp. *mazama*, which lives at higher elevations in the Cascade Range, feeding mostly on lichens during winter. *Myodes gapperi* subsp. *cascadensis* sampled in conifer forests in the Pacific Northwest was found to have ingested more and more diverse hypogeous fungi than other subspecies living in mixed and deciduous forests in the Central and Eastern USA (Maser and Maser 1988). *Myodes* spp. prefer woodlands with abundant ground cover to escape predation. The ground-dwelling and largely herbivorous voles of the genus *Microtus* were found to feed on truffles, too, in both N-Am and Europe; some species were classified as preferential or opportunistic mycophagists. At least in Central Europe they appear to be less mycophagous than *Myodes* spp. (Schickmann et al. 2012).

The Cricetidae-Neotominae diversified in the Nearctic, where some forest-dwelling species occupy ecological niches which are inhabited by wood mice (Muridae) in the old world. Species of the genera *Neotoma* and *Peromyscus* (Neotominae) were found to feed on true truffles, as was *Apodemus sylvaticus* (Muridae) in the Palaearctic (Schickmann et al. 2012).

Pocket gophers (*Geomyidae*) are burrowing occasional mycophagists living in North and Central America (Maser et al. 1988; Taylor et al. 2009). These medium small mammals (body mass ~ 120–250 g) are herbivorous and moderately long lived.

Murids, the most species-rich family of rodents and mammals, diversified in Eurasia, Africa and Australia. The yellow-necked mouse (*Apodemus flavicollis*) was found to feed on two different truffle species in Austria, Europe (from Puberulum group and Rufum group; Schickmann et al. 2012). The diversity of the fungal diet of *A. flavicollis* was only second to the bank vole, *M. glareolus*; however, the degree of mycophagy was significantly lower in the former (Schickmann et al. 2012). *Apodemus flavicollis* are excellent tree climbers; they use their habitat versatilely and exploit various highly nutritious food sources rather opportunistically. The species can be found in different types of forest and also in more open habitat. It was found abundant in early successional regeneration on a windthrow site (Schickmann et al. 2012), indicating that this species may be important for spore dispersal to disturbed forest sites, thereby potentially promoting forest regeneration by increasing available ectomycorrhizal (ECM) fungal diversity.

Most arvicoline rodents are herbivorous, while murine rodents require a richer diet including seeds and invertebrate prey. Anatomy, habitat use and feeding ecology of bank voles are intermediate between other arvicolids and the murine *Apodemus* spp. (Dróżdż 1966; Butet and Delettre 2011).

The arboricolous and relatively long-lived Glirids are restricted to the old world; mycophagy including feeding on *Tuber* sp. was demonstrated recently for the fat dormouse (*Glis glis*; Schickmann et al. 2012). Sciurids are particularly diverse in N-Am, and many are considered preferential mycophagists. Consumption of true truffles was reported in the Sciurinae, tree squirrels of the genus *Sciurus*, red pine squirrels (*Tamiasciurus hudsonicus*) and the northern flying squirrel (*Glaucomys sabrinus*) and in the Xerinae, chipmunks (*Neotamias* spp.), mantled ground squirrel (*Callospermophilus lateralis*) and hoary marmot (*Marmota caligata*) (Table 21.1). In Europe, reports on mycophagy in sciurids are limited to *Sciurus vulgaris*, which has been known for long to collect, cache and consume fungi (Kumerloeve 1968; Grönwall and Pehrson 1984; Lurz and South 1998; Bertolino et al. 2004). Consumption of *Tuber melanosporum* Vittad. by *S. vulgaris* was observed by a truffle grower in SW France (pers comm, Brive, France, 2013).

The fat dormouse and some sciurids are deep hibernators, e.g. marmots and certain ground squirrels. Most notorious mycophagists among the Sciurinae, such as *G. sabrinus* or *S. vulgaris*, do not hibernate. Food caching and hoarding, including truffles (Vernes and Poirier 2007) is a common survival strategy.

Shrews (*Sorex* spp.) are very small mammals feeding predominantly on invertebrate prey, which were only recently reported to consume *Tuber* spp. (Kataržytė and Kutorga 2011; Schickmann et al. 2012). Previously, soricids had been known to feed on *Endogone* spp. and Glomeromycota (Whitaker and Maser 1976; Maser et al. 1978). Ingestion of truffle spores by shrews was suspected to be an accidental side effect of preying on mycophagous invertebrates (Fogel and Trappe 1978; Schickmann et al. 2012). However, the quantity of truffle spores in fecal pellets was comparable in *Apodemus* spp. and *Sorex* spp. (Schickmann et al. 2012). High spore numbers of *Tuber* sp. and of some Russulaceae rather indicate direct consumption of fungal fruiting bodies, albeit possibly infested with insect larvae. Therefore, *Sorex* spp. were considered as selective occasional mycophagists (Schickmann et al. 2012). Inclusion of *Tuber* spp. in the diet of *Sorex* spp. is consistent with relatively high nutritional quality of true truffles (see below).

Maser et al. (1988) and Cázares and Trappe (1994) report the consumption of true truffles by Leporids and Ochotonids, respectively (Lagomorpha). Mycophagous small mammals in other orders (e.g. opossums, Didelphimorphia) might consume true truffles, too, but this has not been documented yet.

## 21.3 Potential Adaptations to Mycophagy and Life History Traits of Small Mammals

Mycophagy requires specific capacities, such as detection of truffles, recognition of edible versus poisonous fungi and effective digestion of fungal biomass. The diversity of mycophagous small mammals (Table 21.1) and the frequency of opportunistic and preferential mycophagy suggest that the adaptive value of mycophagy is commonly sufficient to compensate for the costs associated with adaptations to this diet. Small mammals might be preadapted for mycophagy, e.g. by a well-developed sense of smell, and specific capacities improving the benefits of mycophagy be acquired gradually. Obligate mycophagy, as reported for *M. californicus* subsp. *californicus*, a species with relatively fragile teeth not suitable for more abrasive food items of plant origin, appears to be very rare (Claridge and Trappe 2005). Preferential or occasional mycophagists avoid the risks of strict specialization and respond to the availability of diverse resources in a more versatile, flexible manner.

Life history traits of preferentially mycophagous small mammals are diverse. *G. sabrinus* has characteristic traits of K-selected species (sensu MacArthur and Wilson 1967): relative longevity, late reproduction, low annual fecundity, a long period of maternal investment and density-dependent population growth (Smith 2007). Similar life cycle characteristics are found among other tree squirrels (Sciurinae) and in the arboricolous *G. glis*. Longevity and associated traits of K-selection were attributed to reduced mortality by predation, as facilitated by arboreality (Shattuck and Williams 2010), and, more specifically, by gliding (Holmes and Austad 1994).

Most very small mycophagous mammals, such as red-backed voles (*Myodes* spp.), wood mice (*Apodemus* spp.) and forest-dwelling shrews (*Sorex* spp.), share characteristics of r-selected species: short lifespans of 1–2 seasons and prolific reproduction resulting in highly fluctuating populations, typically peaking in autumn (Gliwicz and Taylor 2002). Fast life cycles are considered a response to high extrinsic mortality rates, and furthermore they facilitate rapid adaptation of population sizes to food abundance (Bielby et al. 2007).

Body size, energetics and life history traits are generally correlated (Lovegrove 2000). Kleiber's law describes the relationship of body mass and metabolic energy demand, scaling with the three-fourth power of size. The metabolic cost of endothermy is increasingly high in temperate, boreal and subarctic regions, since mass-specific metabolic rates increase with decreasing body size and with increasing latitude. Small mammals in the Palearctic and Nearctic, which comprise most of the known distribution area of the genus *Tuber*, have particularly high size-corrected basal metabolic rates, compared to other zoogeographical zones (Lovegrove 2000). Allometric theory predicts that the digestive capacity of small mammals is constrained by body size and energy demands and that they need to select diets of high digestibility and nutrient quality (Johnson 1996), consistent with the observation that the lower limit of miniaturization of herbivorous mammals (e.g. *Microtus*) is at about 15 g (Gliwicz and Taylor 2002).

Extremely small mycophagous mammals such as *Sorex* spp. may be most informative concerning size-related physiological and ecological constraints acting in evolution. Shrews are highly specialized predators of invertebrates; body sizes are at the lower limit of mammal body size distribution (e.g. *S. minutus*, body mass ~ 4 g), and lifespans are short, typically less than 18 months. Mass-specific metabolic rates are extremely high; therefore, shrews require a high and continuous supply of highly nutritious food. Shrews consume up to 200 % of their body weight per day and can't afford extensive alimentary tracts or extended periods of gut passage. Without access to food, the animals starve rapidly (Hanski 1984). Shrews do not accumulate body fat reserves; nearly all the adipose tissue is brown adipose tissue, which serves for converting metabolic energy into thermal energy by non-shivering thermogenesis (Nieminen and Hyvärinen 2000). Hibernation is absent in shrews; instead, they continue foraging throughout winter, when energy costs of maintaining homeothermy are highest. A reduction of energy requirements is achieved by shrinking body size during winter (Hanski 1984). Short-time food caches assist in securing a continuous food supply.

Due to a solitary lifestyle, strict territoriality and short lifespan, *Sorex* spp. are unlikely to adapt their diet choice by learning; foraging behaviour most probably relies on innate and algorithmic cues. Poorly differentiated digestive systems resulting in limited capacity of digestion suggest that extremely small mammals are constrained to select diets of high digestibility and nutrient quality. These constraints are consistent with selective mycophagy on a subset of truffle species observed in *Sorex* spp. (Schickmann et al. 2012). The finding that the predominantly insectivorous shrews use truffles as a food source challenges the view that these are of low nutritional quality and raises the question whether shrews select truffle species of highest nutritional quality.

Preferential mycophagists are found along the entire r-K continuum in rodents, from *G. sabrinus*, an outstanding example of K-selection, to the mostly r-selected mammals of very small body size. Apparently, the mutualistic relationship between hypogeous fungi and small mammals is flexible and robust enough to be largely independent of the life cycle traits of main mycophagists. The evolution of life cycle characteristics appears to be lineage specific (phylogenetically conserved) and driven by top-down control (predation) rather than by bottom-up factors (food choice and supply; Prevedello et al. 2013).

Daily torpor and hibernation are widespread strategies to save energy in times of food shortage by temporarily abandoning euthermia. Hibernation results in a seasonal interruption of foraging, in contrast to daily torpor. Hibernation is rare or absent among very small mammals, such as *Myodes* spp., *Apodemus* spp. and *Sorex* spp., and among tree squirrels (Sciurinae), but common in ground squirrels (Xerinae), including preferential mycophagists such as *C. lateralis* (Ruf and Geiser 2015). *Glis glis*, an exemplary hibernator, was recently confirmed as mycophagous (Schickmann et al. 2012).

## 21.4 Truffles as a Diet

The nutritional quality of hypogeous fungi was discussed controversially (Claridge and Trappe 2005). Various lines of evidence and theoretical considerations support the dietary relevance of mycophagy in situ: (1) Fungi account for a major part of the food of certain small mammal species (e.g. 72 % of the yearly dietary volume in *Eutamias townsendii*; Fogel and Trappe 1978). (2) Positive relationships between the degree of mycophagy and diverse fitness parameters were observed, e.g. acquisition of hibernation fat in *Eutamias* chipmunks (Tevis 1952), body condition and fecundity of Tasmanian bettong (*Bettongia gaimardii*; Johnson 1994) and juvenile recruitment in *Sciurus alberti* (Dodd et al. 2003). (3) Truffle abundance and frequency was found to be the best predictor of population density of the highly mycophagous northern flying squirrel in Douglas-fir forests of various habitat characteristics (Gomez et al. 2005). (4) Isotopic evidence suggests that most organic C and nearly all N is derived from hypogeous fungi in the northern bettong (*Bettongia tropica*) (McIlwee and Johnson 1998). (5) The nutrient composition of fungi is complementary to a plant-based diet and can compensate for potential deficiencies of the latter concerning amino acid composition, vitamin D and trace minerals such as selenium (Claridge and Trappe 2005). (6) Fungi are present in habitats such as dense forests where other food source of high nutritional quality is scarce or highly seasonal. (7) The net nutritional value of truffles depends on foraging costs, which may be relatively low in terms of energy, time and predation risk when feeding on truffles (Fogel and Trappe 1978). (8) Seasonal and annual variation in fungal fruiting body production is relatively independent from variation of other major food items, e.g. mast; mycophagy can compensate for poor mast. Survival in times of hardiness and during population bottlenecks is of high selective value.

The risks and drawbacks of mycophagy need to be considered, too: many species of macrofungi are toxic, particularly when consumed raw; therefore, recognition of edible species is critical. Seasonal and annual variations in fungal fruiting are high, and nutrient availability is limited.

Experimental evidence from feeding experiments with captive small mammals showed negative (Cork and Kenagy 1989a) or marginally positive (Claridge and Cork 1994; Bozinovic and Muñoz-Pedreros 1995; Dubay et al. 2008) balances for N and energy, depending on the selection and diversity of species tested. Mixed diets of plant and fungal material were modelled to provide a more balanced nutrition than monospecific diets (Bozinovic and Muñoz-Pedreros 1995): truffle diversity is likely to be essential for the mycophagists' nutrition, consistent with the diversity of fungal species observed in many studies of mycophagy (e.g. Carey et al. 2002). Infestation of fungal fruiting bodies with insect larvae may provide a supplementary nutrient source (Bozinovic and Muñoz-Pedreros 1995). Even if the quantitative contribution of mycophagy to nutrition is limited (occasional mycophagy), fungi might serve as a dietary supplement which provides rare nutrients (see below).

## 21.5 Nutritional Value and Absence of Toxicity in True Truffles

Available data indicate a wide range of nutritional value within the diversity of epigeous and hypogeous fungi (Wallis et al. 2012) and within the genus *Tuber*. Orczán et al. (2012) found considerable differences in the mineral composition of diverse ascomycete and basidiomycete genera of hypogeous fungi. Notably, culinary species in the genera *Tuber* and *Mattirolomyces* had higher contents of P, K and Ca compared to other hypogeous fungi. Dry weight soluble protein content in ascomata of four culinary truffle species ranged between 8.7 ± 0.83 % for *T. melanosporum* and 25.0 ± 0.86 % for *Tuber magnatum* Pico. Values for *Tuber aestivum* Vittad. and *Tuber borchii* Vittad. were intermediate. Proteins were of high digestibility (Saltarelli et al. 2008), containing all essential amino acids including some (methionine, cystine, tryptophan and lysine) which are commonly limiting in many food sources of plant origin (Coli et al. 1990). Antioxidant activity of phenolic compounds contained in culinary truffles may offer additional fitness benefits (Villares et al. 2012).

True truffles are not toxic to humans, even when consumed raw. Edibility of fresh, untreated fungi is rather the exception than the rule. Among the epigeous relatives of truffles, *Helvella* and *Gyromitra* are known to cause various symptoms of intoxication when ingested raw or insufficiently processed. Gyromitrin was identified as causative agent of intoxications with *Gyromitra esculenta* (Pers.) Fr. (List and Luft 1968) and later found in many other ascomycetes (Andary et al. 1985), including *Helvella* spp. Gyromitrin is unstable and releases the toxic volatile monomethylhydrazine. It seems that gyromitrin is effective in preventing the consumption of these fungi by mammals, since traces of mammal mycophagy are usually absent even when *Gyromitra* or *Helvella* fruit abundantly (Alexander Urban, unpublished observation). Given the phylogenetic relationships of Discinaceae, Helvellaceae and Tuberaceae (e.g. Læssøe and Hansen 2007), it is possible that the epigeous ancestors of Tuberaceae contained gyromitrin and that the absence of gyromitrin in true truffles is an adaptation to mycophagy.

## 21.6 Digestion

Relatively simple gastrointestinal systems and short processing times suffice to digest high-quality forage. With decreasing digestibility and increasing fibre content, optimal digestion time and the importance of fermentation by gastrointestinal microbes increase. To satisfy their high mass-specific energy requirements, small mammals can increase throughput at the expense of optimal digestion efficiency. When analyzing fecal pellets of small rodents, starch granules staining with Lugol's iodine solution can be observed rather frequently, indicating that digestion is not perfect.

The preferential mycophagists *M. gapperi* and *G. sabrinus* reach about 70 % mean dry matter digestibility when feeding on diverse hypogeous fungi (Dubay et al. 2008). Nitrogen digestibility was 12.3 % and 24.9 % for squirrels and voles, respectively, confirming that most nitrogen was indigestible (Cork and Kenagy 1989a). Claridge et al. (1999) found that *M. californicus* and *G. sabrinus* were able to digest approximately 67 % and 66 %, respectively, of the dry matter from fruiting bodies of *Rhizopogon vinicolor* A.H. Sm. Apparent N digestibility was 35 % and 11 % for voles and squirrels, respectively. The greater assimilation of fungal N by voles than by the much larger squirrels indicates that the digestive systems of voles are very effective relative to their body size (Claridge et al. 1999; Dubay et al. 2008). The golden-mantled ground squirrel (*C. lateralis*) lost weight when fed with *Elaphomyces granulatus* Fr.; dry matter digestibility was approximately 60 % (Cork and Kenagy 1989a).

In addition to allometric constraints, important variation in the digestive capacities and nutritional requirements of small mammals of comparable size was found, linked to evolutionary history and specific adaptations of dietary physiology and anatomy. Differences in food choice and digestive capacity between arvicolid and murine rodents may serve as an example. The arvicolid bank voles, recently confirmed as preferential mycophagists (Schickmann et al. 2012), have a better capacity to digest low-energy food than the murid *Apodemus* spp. (Butet and Delettre 2011). Voles were found more effective in extracting N from fungal sources than squirrels, which may be explained by specific adaptations of the caecum. Maintenance nitrogen requirements in flying squirrels were lower than predicted by allometric equation. Northern flying squirrels did not prefer diets high in N, in contrast to red-backed voles. Saving nutrients might be an alternative strategy which allows to subsist during winter on poorer alternative food sources such as lichens (Dubay et al. 2008). Among mycophagous marsupials, a differentiated foregut is a common adaptation to improve the digestion of fungal forage (Claridge and Cork 1994).

Concentrate selection is a successful strategy of combining high throughput with high digestion efficiency. In concentrate selecting hindgut fermenters, increasing use of fibrous diets correlates with increasing relative size and complexity of the caecum and/or proximal colon which facilitate the selective retention of solutes and small particles (Cork 1994). *Microtine* rodents which have complex hindguts and separate digesta in the caecum are able to use food of low digestibility (down to 30 %). Intakes of dry matter by sciurids and murids, which apparently lack separation mechanisms, are consistently lower than those of microtines at digestibilities below ~ 70 %. Caecotrophy is typically combined with coprophagy (Sakaguchi 2003).

The gut systems of the insectivorous shrews differ importantly from the rodents: the post-gastric tract is relatively short (2–6 × head and body length), the caecum is reduced or absent, differentiation between small and large intestines is small and retention times are short, to cope with the extremely high mass-specific energy demands of shrews. These adaptations imply that high-quality food is needed for efficient digestion. Selectivity of mycophagy in shrews (Schickmann et al. 2012) may be a response to their specific requirements of higher-quality food. It is noteworthy that *Tuber* sp. was highly preferred by *Sorex minutus* (Schickmann et al. 2012), one of the smallest and probably most demanding species.

## 21.7 Food Choice: Selection of True Truffles?

There is variation in olfactory signals, nutrient content, seasonal availability, abundance and size among and within genera of hypogeous fungi. The question arises whether harvest and consumption of hypogeous fungi are neutral or selective (Johnson 1994). Theory would suggest that mycophagists preferentially forage for easily detectable, abundant and nutrient-rich fruiting bodies. Over evolutionary timescales, selection by mycophagist may have resulted in increased attractivity. From an anthropocentric perspective, culinary truffles are most attractive. This appreciation appears to be supported by data on the nutrient content of truffles (Orczán et al. 2012). Do small mammal mycophagists prefer the genus *Tuber* and, more specifically, the culinary species?

*Glaucomys sabrinus* was frequently reported to consume a diverse array of hypogeous fungi, but with a consistent preference for certain basidiomycete genera rich in P and K (*Gautieria*, *Rhizopogon*, *Gastroboletus*) (Zabel and Waters 1997; Lehmkuhl et al. 2004; Meyer et al. 2005; Dubay et al. 2008). True truffles appeared to be negatively selected by *G. sabrinus* (Gomez et al. 2005). Red-backed voles (*M. gapperi*) preferentially ingested *Hydnotrya variiformis* Gilkey, which is rich in N and lipids (Dubay et al. 2008). Schickmann et al. (2012) found that a species of Puberulum group was highly preferred by *S. minutus*.

## 21.8 Foraging Behaviour in Small Mammals and Dispersal of Truffle Spores

True truffles were detected in many studies of small mammal mycophagy (Table 21.1), but mostly at relatively low frequency (0.1–5 %), compared to the most abundant hypogeous basidiomycetes (e.g. *Rhizopogon* spp. in some coniferous forests). Seasonal, annual and habitat-specific variations of *Tuber* spore frequency are high and likely reflect variation in truffle availability. In addition, abundance of alternative diets (e. g. mast) influences foraging behaviour and food choice in the highly versatile small mammals. Low frequency implies that detection probability is highly dependent on sampling density, leaving an important role to chance and stochastic variation. In many studies, detection of *Tuber* spp. was site or season specific, in contrast to other, more frequent basidiomycete genera. Studies in ecosystems where true truffles are dominant, including plantations, are needed to obtain more data on mycophagy and true truffles.

Foraging behaviour of many small mammal species is highly flexible and adaptive. Home range size, microhabitat use and foraging behaviour influence the retrieval of truffles and the dispersal of truffle spores. Small mammals most likely rely on olfactory (Talou et al. 1990; Donaldson and Stoddart 1994) and tactile sensory perception when foraging for truffles. The visual sense is well developed in more arboreal species and may be reduced in strictly ground-dwelling species.

Evolution of a high degree of mycophagy can evolve in species with different habitat use; a ground-dwelling lifestyle of small mammals does not necessarily imply a higher degree of mycophagy, compared to more arboreal species. Many avid small mammal mycophagists are tree climbers (e.g. tree squirrels and flying squirrels, common dormouse, wood mice and, to some extent, bank voles) and most are nocturnal. Home range size, habitat use and complexity of foraging behaviour vary with body size, dietary specialization and phylogenetic affinity of small mammals. Small rodents are important prey of various predators, including diverse carnivores and birds of prey. Predation of mycophagists may result in accidental spore dispersal over longer distances, since the home ranges of predators are usually much larger than the home ranges of their prey.

Small mammals appear to be very efficient in locating hypogeous fungi of different species, and at least some species of hypogeous fungi are consumed quantitatively (Johnson 1994). Typically, small mammals consume more different species of hypogeous fungi than a specialized mycologist can find in a given area (Johnson 1996; Schickmann et al. 2012); therefore, the study of mycophagy holds promise in providing new data on local diversity and biogeography of hypogeous fungi. The diversity of fungal spores contained in fecal pellets may have multiple reasons: some small mammal species most likely eat all species they find and recognize as edible, to minimize foraging effort; in that case the diversity of fungi ingested would be representative of the diversity of fungal species encountered. Some species, such as *G. sabrinus*, select the most preferred species (Zabel and Waters 1997; Lehmkuhl et al. 2004; Meyer et al. 2005; Dubay et al. 2008). The diversity of spores encountered in fecal pellets may be higher than the diversity of fungi consumed at a given time, due to long retention times and mixing of fungal spores in the caecum. Cork and Kenagy (1989b) calculated mean retention times of *E. granulatus* spores in the gut systems of golden-mantled ground squirrels (*Spermophilus saturatus*; $31.8 \pm 2.4$ h) and deer mice (*Peromyscus maniculatus*; $12.0 \pm 2.4$ h). Ninety-five percent egestion required $52 \pm 2$ h in *S. saturatus*. Spore retention in the digestive tract of mycophagous rodents affects the temporal and spatial dynamics of spore dispersal (Danks 2012) and may result in an overestimation of the short-time diversity of truffle consumption. However, analyses of stomach contents, which can be expected to be more representative of most recent feeding activity than spore counts in fecal pellets, typically reveal diverse feeding habits, too (e.g. Maser and Maser 1988).

Many small mammals, including preferential mycophagists such as *Myodes* spp. or *G. sabrinus*, cache food, either as larder hoarders or as scatter hoarders, and fungi are no exception (Vernes and Poirier 2007). Shrews maintain short-time food caches, to satisfy their need of continuous food supply. Squirrels dry fungi on tree branches; sun exposure massively increases vitamin D content in dried fungi (Maser et al. 2008). Pilferage of caches and re-caching by conspecifics or by different animal species (e.g. birds) is not uncommon and may further extend and entangle the mycophagy network (Maser et al. 2008).

Recognition of edible species is vital when foraging on potentially toxic food, such as fungi. The short lifespan of very small mammals implies that individuals will continue to encounter new truffle species during one season or two seasons at most. Most likely, recognition of edible fungal species is based on innate and possibly generic olfactory clues and individual experience. The lifespan of sciurids can extend over several years; therefore, learning, experimentation and imitation of conspecifics might be more relevant.

## 21.9 Seasonality in Mycophagists and Truffles

Small mammal populations are limited by food supply and predation (Prevedello et al. 2013). Cyclic overpopulation of small mammals and poor seed crops likely enhance the importance of mycophagy in reducing periodical food stress (Fogel and Trappe 1978). Seasonal build-up of rodent populations may coincide with fungal fruiting peaks in late summer and autumn. Individual species of truffles may be available for restricted periods only, but collectively, the production of hypogeous fruiting bodies throughout the year provides a more reliable food resource for small mammals (Maser and Maser 1988).

The periods of the year which are most critical for survival differ according to overwintering strategies. In hibernating species such as *G. glis* and certain sciurids, food availability in autumn and spring is most important. Small non-hibernating species such as shrews (*Sorex* spp.) and red-backed voles (*Myodes* spp.) depend on a continuous food supply during winter. Hoarders like many sciurids and murids can use the available resources more flexibly.

The diversity of hibernation strategies implies that different species of small mammals are available as vectors of truffles at different seasons. In periods of food shortage, fungal food may be most important for survival and most readily eaten and vectored. Seasonal variation in the availability and activity of small mammal vectors likely is a factor of selection acting on truffle phenology.

## 21.10 Mycophagy, Truffles and Plant Community Succession

Mycophagy may contribute to plant establishment and vegetation succession, whenever supply of mycorrhizal fungal inoculum is limiting, thereby influencing forest ecology, diversity and productivity (Johnson 1996; Maser et al. 2008; Schickmann et al. 2012). The provision of mycorrhizal inoculum can be critical for plant establishment during succession after major disturbances (Allen et al. 1992). Terwilliger and Pastor (1999) demonstrated that spore dispersal of hypogeous fungi by red-backed vole (*M. gapperi*) promotes the invasion of conifers into meadows formed in abandoned, drained beaver ponds. Cázares and Trappe (1994) showed that various mammal species are vectors of ECM hypogeous fungi (incl. *Tuber*) in successional vegetation close to a receding glacier forefront. Schickmann et al. (2012) found specific communities of small mammals and truffles including true truffles in early successional forest regeneration after stand-replacing windthrow. *Tuber whetstonense* J.L. Frank, D. Southw. and Trappe was frequently found in fecal pellets of small rodents trapped in *Quercus garryana* Dougl. savanna at up to 35 m distance from mature oak trees. *Tuber candidum* Harkn. was present as mycorrhiza in mature trees and experimental seedlings and occasionally in fecal pellets, too (Frank et al. 2009). *Tuber californicum* Harkn. and *Tuber* sp. were part of the ECM community developed on the roots of bioassay seedlings grown in soil collected immediately after stand-replacing wildfire, indicating that propagules of true truffle species survived the fire in the soil spore bank (Taylor and Bruns 1999). However, it was not assessed whether these propagules were animal-dispersed spores.

Various truffle species are found in different types and successional states of vegetation; certain species grow best in earlier stages of forest development and are less competitive in mature undisturbed forests with closed canopy (e.g. Schickmann et al. 2012). If early successional and certain post-disturbance states of woodland development are optimal for the growth of certain species of true truffles (e.g. Schickmann et al. 2012), efficient colonization of these optimal habitats is critical for the species' reproduction. Different truffle species may be prevalent in the ECM state and in the spore population dispersed by mycophagists, at least within a given time frame (Frank et al. 2009).

Typical preferential mycophagists are adapted to living in closed forest with abundant shelter. Small mammals have relatively small home ranges, which may limit their dispersal potential. Therefore, their capacity to colonize and distribute spores to massively disturbed habitats may be limited. More opportunistic species with flexible habitat use (Maser et al. 2008; Schickmann et al. 2012) and larger mammals (Piattoni et al. 2012) are probably more effective in colonizing such types of habitat.

## 21.11 Small Mammal Mycophagy, Truffle Cultivation and the Truffle Life Cycle

As major consumers of plant, fungal and small animal biomass, small mammals have multiple direct and indirect effects on true truffles, their host trees and habitats, in natural truffle grounds as in plantations. The burrowing activity of many small mammal species disturbs the soil and is likely to be beneficial for pioneer species, including certain species of true truffles. Soil disturbance reduces herbal vegetation cover, potentially assisting in the formation of brûlés, and can improve water retention, by improved infiltration and reduced capillarity (Maser et al. 2008).

Voles like the common vole (*Microtus arvalis*) can cause damage to host trees in young truffle plantations, particularly when population sizes are high (Urban et al. 2012). Voles, like other small mammals, are important prey of many different predators, such as various species of birds of prey, owls, red fox (*Vulpes vulpes*), wildcat (*Felis silvestris*) and mustelids such as weasel (*Mustela nivalis*), European polecat (*Mustela putorius*) and European badger (*Meles meles*). Providing habitat for the predators is a natural way of keeping rodent populations at an acceptable level.

Insectivorous (*Sorex* spp.) and omnivorous (*Apodemus* spp., *M. glareolus*) small mammals may improve the fitness of the truffles' host trees by feeding on invertebrates, thereby reducing the pressure of herbivorous and seed-predating insects, e.g. the curculionid *Otiorhynchus* spp.

In natural truffle populations, the importance of small mammal vectoring of truffle spores for the formation of new mycelia is obvious. Gut passage might promote germination of truffle spores, as it was observed in spores having passed through the gut of *Sus scrofa* (Piattoni et al. 2014). In managed plantations, however, the seedlings are already mycorrhized with truffles before planting. When truffles start to grow, small mammals can consume a part of the harvest, redistributing the spores by endozoochory. Is the continuous supply of truffle spores necessary to maintain the productivity of a truffle plantation? This question is linked to the life cycle and population ecology of true truffles. Murat et al. (2013) found relatively small genets of *T. melanosporum* mycelia (less than 5 m distance between ramets of the same genet) in productive truffle plantations. Genet turnover between two consecutive years was found considerable, suggesting that the population structure in truffle plantations is highly dynamic. More surprisingly, diverse genets associated with one host tree were of the same mating type, reducing the probability that genets of opposing mating type get into contact (Linde and Selmes 2012; Murat et al. 2013). This pattern raised the question of the pathways of mating in true truffles, which were only recently reconfirmed as sexual (Paolocci et al. 2006; Murat and Martin 2008). Small, short-lived mycelia originating from meiospores are a possible solution. If this mechanism is true, ascospore dispersal by animal vectors or, alternatively, by orchard management practices is essential for truffle orchard productivity and might be compared to pollination in fruit orchards. Alternatively or additionally, microconidia might act as spermatia. However, this type of spores has been observed in few species of Puberulum group only, thus far (Urban et al. 2004; Healy et al. 2013).

A potential economic drawback of mycophagy in truffle orchards is the dispersal of non-marketable or low-value competing fungi, since mycophagists use to feed on a variety of species of hypogeous fungi (Urban et al. 2012). It can be predicted that following intentional and unintentional (Murat et al. 2008) introductions of true truffles into new habitats, particularly in the southern hemisphere, many new mycophagous mammal species (both marsupials and placentaria) will start to feed on and disperse true truffles, and native ECM host species are likely to get mycorrhized.

## 21.12 Conclusions

True truffles, like most other hypogeous fungi, are involved in two different mutualistic networks, mycorrhiza and mycophagy. These relationships are a key component of forest food webs, which structure forest biodiversity and sustain forest productivity and resilience. They existed throughout the evolution of the genus *Tuber* and can be considered the ultimate causes of characteristic traits of truffles, such as truffle odours and the absence of toxicity.

The synthesis of available literature on the feeding of small mammals on true truffles supports a series of conclusions and hypotheses: (1) Mycophagy is widespread among small mammals, involving a phylogenetically diverse array of species, with diverse nutritional habits, life cycle traits and foraging behaviours. Fidelity to a fungal diet is high among a subset of species and populations. In the natural distribution range of true truffles, red-backed voles and certain species of the squirrel family (Sciuridae) are recognized as preferential mycophagists. (2) Small mammal mycophagy likely accounts for a large proportion of animal-vectored spore dispersal, at least at the local level. (3) The proportion of spores of the genus *Tuber* is low in most forest habitats studied thus far, dominated by basidiomycetes. (4) The nutritional value of true truffles is relatively high, compared to other food items of plant and fungal origin. (5) Nutrient assimilation from hypogeous fungi is variable among small mammal mycophagists and appears to be phylogenetically conserved. (6) Allometric constraints on acceptable food quality potentially limit mycophagy in extremely small mammal species such as *S. minutus* and may be at the origin of more selective mycophagy, which could be a driving force in the evolution of nutritional quality of truffles. Information on food choice among different species of hypogeous fungi is still limited. (7) Small mammal mycophagy is essential for short-distance dispersal and, possibly, mating of true truffles. (8) Progress in DNA metabarcoding of fungal communities in environmental samples offers new opportunities for assessing the diversity of fungi consumed by mycophagists with unprecedented taxonomic resolution.

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