

CHAPTER 17-1

RODENTS – MUROIDEA: MURIDAE

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CHAPTER 17-1

RODENTS – MUROIDEA: MURIDAE



Figure 1. Rodent among mosses and lichens, Auckland Island. Photo by James Russell, with permission.

Mammals

Scattered references to mammals using bryophytes for nests or habitat appeared early in the literature. However, until search engines were able to do the massive reading required to find these, bryologists were able to find little documentation of these uses.

Mammals are warm-blooded animals, so it is logical that in northern climates some of them would use bryophytes as nesting materials, taking advantage of their insulating properties. But as this chapter will reveal, they have found a variety of uses for bryophytes, especially in northern habitats.

Rodentia – Rodents

The term "rodent" is derived from the Latin word *rodere*, meaning to gnaw (Wikipedia 2017a). They comprise the order **Rodentia**, distinct in having a single pair of incisors (cutting teeth) that grow continuously. They comprise 40% of the mammal species and are common and abundant on all continents except Antarctica.

Even larger animals are known to use bryophytes for nesting purposes. But rodents seem to have the most uses. Le Blanc *et al.* (2010) determined that in eastern Canada, moss cover and vertical cover were the predominant influences on community structure of small mammals, whereas for forest birds it was conifer basal area, vertical cover, and snag availability. Kaminski *et al.* (2007), in the

Allegheny Mountains of West Virginia, USA, demonstrated through principal component analysis that moss cover and abundant seedlings were important for specialist rodents in habitats with coarse woody debris.

One can find numerous studies in which mosses were made available as nesting materials in the lab (*e.g.* McGuire & Sullivan 2001; Pulfer 2007). In trapping studies, mosses have been used for insulation and food in the trap (Lentfer 1975; Peterson & Batzli 1975). Those studies that describe actual wild nests are much fewer than might be expected from the lab. Nevertheless, mosses are not uncommon in nests, but they are usually only minor components.

Bryophytes as Food

Until somewhat recently, we assumed that mammals did not eat bryophytes. Batzli and Cole (1979) reported that mosses produced low metabolizable energy for **microtine** rodents (members of the subfamily **Microtinae**, with teeth adapted for herbivory).

Nevertheless, both bovines and rodents use mosses as part of their diets. Prins (1982) observed that in cold environments mosses are eaten by a variety of herbivores, suggesting that the mosses might provide the secondary compound arachidonic acid that would help to keep the membranes of the footpads pliable on the cold ground and snow.

Microtine rodents in northern climates select mosses as part of their diet (Batzli & Jung 1980). Batzli (1983) likewise suggests that it may be secondary compounds that drive these rodents to consume bryophytes – such compounds as arachidonic acid? Or might it be a sort of winter tonic that helps to prevent bacterial infections? The well-known cycling of these northern rodents does not seem to correlate with nutrient fluctuations, and mosses are more difficult for rodents to digest than flowering plants (Tahvanainen *et al.* 1991), but Batzli contends that we cannot rule out secondary compounds for the changes in diet. In addition to making use of arachidonic acid, a fatty acid not found in flowering plants, Prins (1982) reminded us that mosses are high in fiber, low in nitrogen, and low in digestible energy, seemingly giving the rodents little reason to eat them unless the mosses provided something special and important – like arachidonic acid.

This seemingly non-nutritional status of bryophytes is supported by the study of 35 bryophyte species from the high Arctic tundra (Figure 2) of Devon Island, Canada (Pakarinen & Vitt 1974). They demonstrated that the highest nitrogen content is in the green portion, and that the fraction is higher in hydric species than in mesic or xeric species. Mean contents (%) for the green portion of these species are total nitrogen, 1.00 (1.08 ash-free) and total carbon, 45.9 (48.7 ash-free). By contrast, the percent N content of *Nephrophyllidium crista-galli* (a dicot; Figure 3) in Alaska ranged ~3-3.8% in areas where Sitka deer gathered and 2-3% in areas where they were absent (Klein 1965). In the five Arctic tracheophyte species measured for carbon percentage by Tolvanen and Henry (2001), all were inferior to that in the Pakarinen and Vitt (1974) moss study except that of the shrub *Cassiope tetragona* (Figure 4), which was only slightly higher. Barkley *et al.* (1980) and Batzli and Pitelka (1983) consider mosses to have a nutrient content that does not differ from that of other plants in the same region.



Figure 2. Nunavut tundra, Canada. Photo by A. Dialla, through Creative Commons.

Turchin and Hanski (2001) suggested that interaction with the food supply was one possible explanation for rodent cycling in far northern habitats. Nevertheless, based on their models they concluded that predation was the best explanation for population cycling, but they allowed for the possibility of food to play a role in cycles of lemmings, rodents that rely on mosses for food.



Figure 3. *Nephrophyllidium crista-galli*, an Arctic plant with 3-3.8% nitrogen content in Alaska. Photo by Alpsdake, through Creative Commons.



Figure 4. *Cassiope tetragona*, an Arctic plant with nitrogen content only slightly higher than that of mosses. Photo by Bjoertvedt, through Creative Commons.

One example of the role of secondary compounds is the hormonal precursors found in graminoids (Hansson & Henttonen 1988). But that would fail to explain the cycles in shrub and moss eaters. Are we missing something? Both the arctic rodents and the bryophytes reproduce in early spring. Is there a time in winter, or late fall, when bryophytes produce a hormone precursor, if not the hormone itself? Or is it the shift to a greater percentage of bryophytes in the diet that triggers hormone production? Hansson and Henttonen concluded that the cycles are complex, that they are regular in only a minority of the rodents, and that extrinsic factors are important in regulating these cycles.

One of the mechanisms used by the woodrat genus *Neotoma* is that of caching to reduce toxin intake (Torregrossa & Dearing 2009). Although this study did not include bryophytes, it is a topic that should be considered in understanding bryophyte relationships. Among the three non-bryophyte feeders in the study, the white-throated woodrat (*N. albigula*; Figure 5) made a terpene-free cache. In nature, dismantled middens of this species revealed no alpha-pinene, despite its occurrence in the surrounding trees. The desert woodrat (*Neotoma lepida*; Figure 6) instead decreased total food intake, but did not decrease the terpene-containing food. The third species, Bryant's woodrat (*N. bryanti*; Figure 7), did nothing to regulate

terpene intake. Nevertheless, in the food cage all three species abandoned a greater amount of food when it contained terpene.



Figure 5. The white-throated woodrat, *Neotoma albigula*, a species that makes a terpene-free cache. Photo by J. N. Stuart, through Creative Commons.



Figure 6. *Neotoma lepida*, a species that does not decrease terpene-containing foods. Photo by Lloyd Glenn Ingles, through Creative Commons.



Figure 7. Bryant's woodrat, *Neotoma bryanti*, a species that does nothing to regulate terpene intake. Photo by Alan Harper, through Creative Commons.

This raises the question of phenolic compounds in bryophyte food organisms. Some of these are aromatic, suggesting that they will evaporate from the bryophytes with time, or at least decrease in concentration. Do these phenolic compounds also decrease in winter when the bryophytes are mostly inactive? Do stored bryophytes in nests lose their phenolic compounds?

Little is known about seasonal variation in phenolic concentrations of bryophytes. Hribljan (2009; in prep) found no significant change in phenolic concentrations from September to November in the moss *Pleurozium schreberi* (Figure 8) in the Keweenaw Peninsula of Michigan, USA (Figure 9). But do concentrations decrease as the mosses rest under the snow of winter? Do they decrease during hot, dry periods of summer? And if so, do rodents change their feeding habits in response?



Figure 8. *Pleurozium schreberi*, a boreal forest moss that showed no change in phenolic content from September to November. Photo by Sture Hermansson, with online permission.

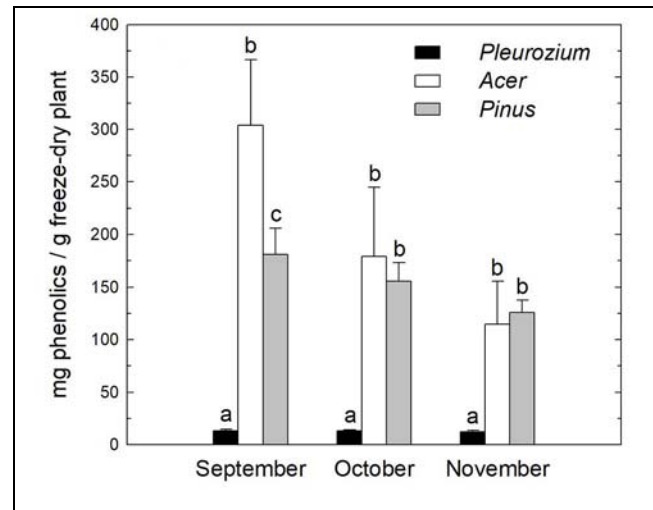


Figure 9. Seasonal phenolics in *Pleurozium schreberi*, leaves of a deciduous maple tree (*Acer*), and needles of the conifer *Pinus*. Drawn by John Hribljan, with permission.

Impacts on Bryophytes

Rodents are common in mires (Bostrom & Hansson 1981) and can be a major influence on bryophyte dynamics there, particularly in boreal and northern climates. Their use of bryophytes as food, the trimming of runways, and

uses for nesting materials all remove bryophytes, sometimes faster than the bryophytes can regrow.

Grazing

Ericson (1977) found that not only the dwarf shrubs and grasses, but also the mosses in northern Sweden were impacted by grazing by small rodents (moles and lemmings). Mean moss cover declined in 1974 and 1975, but experienced a strong increase in 1976. Ericson attributed these changes entirely to grazing and other activities of the microtine rodents. The rodents typically bite off tips of mosses in the snow-free season, but in the snow-covered season they bite the shoots close to the bases.

In 1974, the decrease in mosses was primarily the result of summer grazing and runways (Figure 10), whereas in 1975 it was a further response to these activities during the winter period until the rodent population crash (Ericson 1977). These rodents included primarily the wood lemming *Myopus schisticolor* (Figure 10), a species that prefers mosses (Kalela *et al.* 1963a). The strongest bryophyte declines included the mosses *Ptilium crista-castrensis* (Figure 11) (73%), *Dicranum scoparium* (Figure 12) (57%), *D. polysetum* (Figure 13) (53%), *D. majus* (Figure 14) (37%), *Hylocomium splendens* (Figure 15) (30%), and *Pleurozium schreberi* (Figure 8) (12 %). On the other hand, species on windthrows and tree stumps [*Dicranum montanum* (Figure 16), *Sanionia uncinata* (Figure 17)] were largely spared.



Figure 10. Wood lemming, *Myopus schisticolor*, by its path through *Hylocomium splendens*. Photo by Risto S. Pynnönen through Wikimedia Commons.

Although Kalela *et al.* (1963a) considered *Plagiothecium denticulatum* (Figure 18) to be a rejected species by *Myopus schisticolor* (Figure 10), this species was eaten at least sometimes in the Ericson (1977) study. Ericson also noted that *Pleurozium schreberi* (Figure 8) was not eaten as frequently as its abundance would suggest (see also Kalela *et al.* 1963a, b; Helminen & Valanne 1963). In 1975, the picture was reversed, with *Pleurozium schreberi* decreasing by 19% while *Ptilium crista-castrensis* (Figure 11) increased by 43% and *Dicranum scoparium* (Figure 12) increased by 70%! This decrease-increase trend is a common phenomenon by forest floor mosses, demonstrating a one-year time lag relative to the microtine rodent peak years.



Figure 11. *Ptilium crista-castrensis*, the bryophyte that experiences the strongest decline when in the presence of the wood lemming *Myopus schisticolor*. Photo by Michael Lüth, with permission.



Figure 12. *Dicranum scoparium*, a species that declines in the presence of the wood lemming *Myopus schisticolor*. Photo by Janice Glime.



Figure 13. *Dicranum polysetum*, a species that declines in the presence of the wood lemming *Myopus schisticolor*. Photo by Janice Glime.



Figure 14. *Dicranum majus*, a species that is damaged and declines when wood lemmings are present. Photo by Michael Lüth, with permission.



Figure 15. *Hylocomium splendens*, a species for which cover diminishes in the presence of the wood lemming. Photo through Wikimedia Commons.



Figure 16. *Dicranum montanum*, a species that lives on stumps and tree bases and is spared from damage by wood lemmings. Photo by Michael Lüth, with permission.



Figure 17. *Sanionia uncinata*, a species of stumps and windthrows and that is not harmed by wood lemmings. Photo by Michael Lüth, with permission.



Figure 18. *Plagiothecium denticulatum*, a species that is rejected by the wood lemming *Myopus schisticolor*. Photo by Michael Lüth, with permission.

Weft and other dominant species growth forms benefit from the rodents through regeneration from rhizomes in *Polytrichum commune* (Figure 19) and *P. juniperinum* (Figure 20) (Meusel 1935; Wigglesworth 1947) and *Dicranum* spp. (Figure 12-Figure 14, Figure 16) (Meusel 1935), from broken or bitten tips of *Hylocomium splendens* (Figure 21) (Correns 1899), and from isolated leaves and leaf fragments of *Dicranum* spp. and *Polytrichum commune* (Correns 1899).



Figure 19. *Polytrichum commune*, a species that regenerates from rhizomes. Photo by A. J. Silverside, with permission.



Figure 20. *Polytrichum juniperinum*, a species that regenerates from rhizomes. Photo by Janice Glime.



Figure 21. *Hylocomium splendens*, a species that exhibits broken and bitten tips when rodents feed on it. Photo by Amadej Trnkoczy through Creative Commons.

Hansson (1969) reports frequencies of 86, 90, and 50% mosses in the diet of the bank vole *Myodes glareolus* (Figure 22) in Sweden in three successive years, and mosses form a regular part of the diet in all seasons (Hansson 1971). Contrarily, Holisová (1966) found only traces of mosses in their diet in lowland oak forests. Kalela (1957) found that *Pleurozium schreberi* (Figure 8) is especially eaten by the grey red-backed vole *Myodes rufocanus* (Figure 23), although mosses form only a minor part of the diet.



Figure 22. *Myodes glareolus*, bank vole, eating mosses in the Netherlands. Photo by Andrew Spink, with permission.



Figure 23. *Myodes rufocanus* (grey red-backed vole), a vole that eats the moss *Pleurozium schreberi*. Photo by Zbyszek Boratynski, through Creative Commons.

Hansson (1969) likewise reported a high frequency of mosses in the diet of the field vole *Microtus agrestis* (Figure 24) at Ammarnäs in Scandinavia, although he found that they usually contribute only a minor part of the diet elsewhere. Grazing by rodents during their peak years was so great in Scandinavia that moss cover declined significantly, many plots by more than 50%, for two consecutive years (Ericson 1977).



Figure 24. *Microtus agrestis* (field vole) among mosses. Photo from Wikimedia Commons.

Experimental evidence in England supports the role that small rodents can have in altering the vegetation. Summerhayes (1941) used areas that were fenced with fine mesh wire to keep the field vole *Microtus agrestis* (Figure 24) out. Control plots were similar but lacked the fencing. The original plots had mostly the grass *Melica caerulea* (Figure 25), but also the grasses *Holcus mollis* (Figure 26) and *Deschampsia caespitosa* (Figure 27). The enclosures resulted in almost total disappearance of mosses within them during the sampling period of 1932 to 1939. Summerhayes attributed this to the increased competition by the dominant plants when the vole attack was prevented.



Figure 25. *Melica* sp., the primary ground cover when vole exclosures were erected. Photo from iNaturalist, through Creative Commons.



Figure 26. *Holcus mollis*, one of the plants in the habitat of *Microtus agrestis*. Photo by James K. Lindsey, through Creative Commons.



Figure 27. *Deschampsia caespitosa* in winter, one of the plants in the habitat of *Microtus agrestis*. Photo by Sten Porse, through Creative Commons.

Virtanen *et al.* (1997) similarly established exclosures against the Norwegian lemming (*Lemmus lemmus*; Figure 28) in the late snowbeds of Finnish Lapland. Eight years later they found considerable changes in the vegetation. Mosses had expanded their coverage. *Polytrichum* (Figure 19-Figure 20) species had reached a carpet that was three times as thick as that in the open areas. The mosses experienced vertical growth in undisturbed conditions. Inside the exclosures the liverworts and some prostrate **tracheophytes** (lignified vascular plants) were absent. The open (disturbed) plots were the only place where the bryophytes with good colonizing ability occurred.



Figure 28. *Lemmus lemmus* on *Sphagnum*. Photo by Andreeze, through Creative Commons.

Lemmings in North America can consume up to 90% of the primary production during a peak population year (Schultz 1968; Moen *et al.* 1993). In Scandinavia, they consumed 66% of the mosses and only 33% of the graminoids during these peaks (Moen *et al.* 1993) Bryophytes are a winter staple for the Norwegian lemming (*Lemmus lemmus*; Figure 28) (Virtanen 2000). After 5 years in an exclosure (Figure 29) experiment in a mountain snowbed of northwestern Finland, absence of grazing by lemmings and reindeer (*Rangifer tarandus*; Figure 30) caused an increase in moss biomass (Figure 31). After 15 years, the moss family **Polytrichaceae** (Figure 19-Figure 20) still dominated, but some of the graminoids had also increased (Figure 31). On the other hand, the moss *Kiaeria* (Figure 32) decreased or became completely absent in the exclosures, apparently due to competition from

tracheophytes. Virtanen concluded that the assumption that herbivore grazing in low productivity environments was of little consequence was an incorrect assumption. Grazers can have a significant impact on both bryophytes and tracheophytes in these environments.

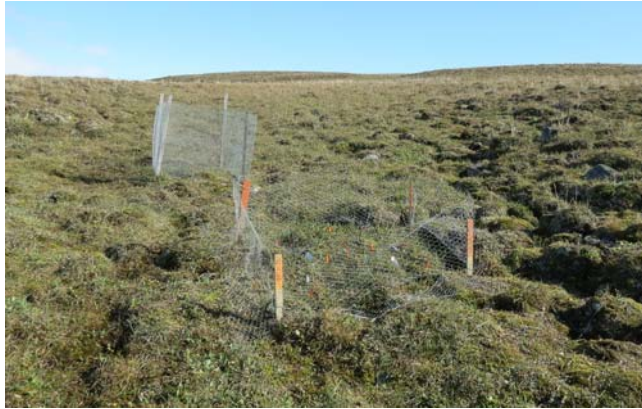


Figure 29. Lemming enclosure 1x1 m on Bylot Island. Photo courtesy of Dominique Fauteux.



Figure 30. *Rangifer tarandus* (reindeer), a species that often co-exists with lemmings and negatively impacts moss biomass. Photo by Dean Biggins, USFWS, through public domain.

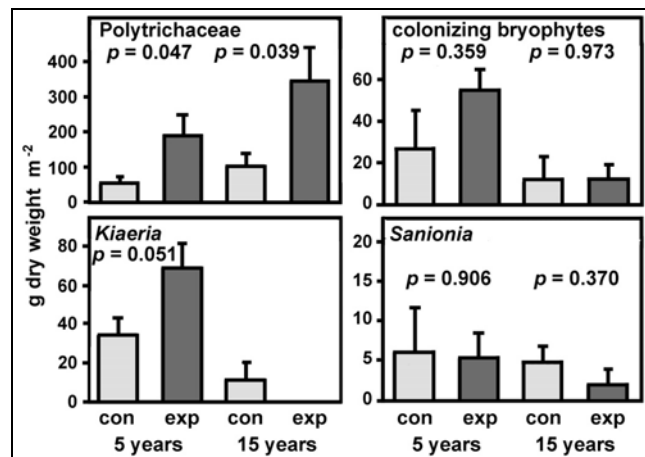


Figure 31. Dry weight of bryophytes after 5 and 15 years in controls (con) and exclosures (exp). Modified from Virtanen 2000.



Figure 32. *Kiaeria starkei*, a moss that benefits from grazing by mammals. Photo by Michael Lüth, with permission.

Andersson and Jonasson (1986) conducted a similar study on rodent exclosures in the alpine heath of Lapland in northern Sweden. Several plants were greatly reduced by the rodents and flowering frequency of food plants decreased. The lemmings (*Lemmus lemmus*; Figure 28) and voles (*Myodes*; Figure 22-Figure 23) both eat the mosses *Polytrichum commune* (Figure 19) and *P. juniperinum* (Figure 20) (Kalela 1957, 1962; Koshkina 1962; Kalela & Koponen 1971; Kalela *et al.* 1971). Andersson and Jonasson (1986) found that *Polytrichum* declined, but they attributed the decline to depression by luxurious growth of tracheophyte species. The *Polytrichum* species have a slower growth rate than that of tracheophytes.

It is the lemmings that make mosses a large part of their diet, differing considerably from the vole diet (Kalela 1957, 1962; Koshkina 1962; Stoddart 1967; Kalela *et al.* 1971, Kalela & Koponen 1971, Baltruschat & Uberbach 1976). Hence, Andersson and Jonasson (1986) concluded that the voles and lemmings may not experience severe competition for food.

The grazing causes good and bad years for bryophytes, sometimes permitting tracheophytes to get established. These tracheophytes can sometimes out-compete the bryophytes. Thus, the rodents can have a major impact on the construct of the vegetation.

Runways, Burrows, and Nests

But consumption is not the only influence on the changing bryophyte communities. The runways and exposed tunnels (Figure 33) are colonized by mosses (Figure 34), especially *Ceratodon purpureus* (Figure 35), *Plagiothecium curvifolium* (Figure 36), *P. denticulatum* (Figure 18), *Pohlia nutans* (Figure 37), and *Brachythecium starkei* (Figure 38) (Ericson 1977). These small turf or mat species are unable to colonize the wet-moss-covered areas and benefit from the disturbance of the runways. The runway species also differ from those of windthrows that are colonized by *Amblystegium serpens* (Figure 39), *Sanionia uncinata* (Figure 17), and *Dicranum montanum* (Figure 16).



Figure 33. *Microtus* and *Apodemus* tunnels, illustrating destruction of the vegetation. Photo by Marijke Verhagen, Saxifraga, with online permission.



Figure 36. *Plagiothecium curvifolium*, a colonizer on rodent runways. Photo by Michael Lüth, with permission.



Figure 34. *Microtus* and *Apodemus* tunnels, showing colonization by mosses. Photo by Marijke Verhagen, Saxifraga, with online permission.



Figure 37. *Pohlia nutans*, a colonizer on rodent runways. Photo by Michael Lüth, with permission.



Figure 35. *Ceratodon purpureus* with immature capsules, a colonizer on rodent runways. Photo courtesy of Dale Sievert.



Figure 38. *Brachythecium starkei*, a colonizer on rodent runways. Photo by Michael Lüth, with permission.



Figure 39. *Amblystegium serpens*, a colonizer of windthrows. Photo by Michael Lüth, with permission.

The role of these rodents in leafy liverwort population dynamics is less clear. Kalela *et al.* (1963a) reported that *Myopus schisticolor* (Figure 10) rejected *Ptilidium ciliare* (Figure 40), but it appears that *Barbilophozia lycopodioides* (Figure 41) experiences at least some foraging. Both species are poor competitors that are able to colonize the exposed substrate of the runways.



Figure 40. *Ptilidium ciliare*, a species rejected by *Myopus schisticolor*. Photo by Li Zhang, with permission.



Figure 41. *Barbilophozia lycopodioides*, a leafy liverwort that is sometimes eaten by rodents. Photo by Michael Lüth, with permission.

Duncan (1954) found that rodents compress the *Sphagnum* (Figure 42) and reduce its growth rate. Duncan found more seedlings (11% germination) of black spruce (*Picea mariana*; Figure 43) on the "fine" mosses [*Mnium* (Figure 44), *Drepanocladus s.l.* (Figure 45), *Helodium* (Figure 46)] compared to non-compressed *Sphagnum* (4.5%). However, compressed *Sphagnum* mats appear to be the best of these substrata for black spruce seedlings.



Figure 42. *Sphagnum magellanicum*, in a genus that gets compressed by rodent "traffic." Photo by Michael Lüth, with permission.



Figure 43. *Picea mariana* sapling in a bed of *Sphagnum*. Photo by Joseph OBrien, USDA Forest Service, through Creative Commons.



Figure 44. *Mnium hornum*, in a moss genus that can provide microhabitat for black spruce germination. Photo by Michael Lüth, with permission.



Figure 45. *Drepanocladus exannulatus*; black spruce seeds can germinate among some members of this genus. Photo by Michael Lüth, with permission.



Figure 46. *Helodium blandowii*; black spruce seeds can germinate among branches of this species. Photo by J. C. Schou, through Creative Commons.

Tabata and Iwasa (2013) found that Smith's red-backed vole, *Phaulomys smithii*, occurred in rocky terrains at the base of Mt. Fuji, Japan, where bryophytes were common. But the role of these rodents in promoting the growth of the bryophytes or in distributing them remains unknown.

Otomys sloggetti (Muridae; Figure 79) typically occupies rocky habitats, living in crevices in nests of weeds and grass (Lynch 1989). However, in boggy and spongy habitats of South Africa, they occupy extensive burrow systems similar to those of *Parotomys brantsii* (Figure 47). The area is characterized by numerous hummocks that are ~200 mm high and ~300 mm in diameter. Lynch (1992) suggested that the moles (*Cryptomys hottentotus*; Figure 48) were the engineers of the hummocks. But it appeared that *O. sloggetti* further enlarged and cleaned them, creating greater habitat variety and colonization by a greater variety of plants, including mosses. The mosses become repeatedly "top-dressed" with soil, creating the hummocky landscape. However, not all agree with this interpretation of the hummock origin, suggesting instead that such non-animal agents as freeze-thaw cycles could account for the hummocks (van Zinderen Bakker & Werger 1974).



Figure 47. *Parotomys brantsii*, Brant's whistling rat, South Africa, nibbling on grass. Photo by Derek Keats, through Creative Commons.



Figure 48. *Cryptomys hottentotus*, a hummock-building vole that prepares the way for Photo by Daderot, through Creative Commons.

The tiny moss *Acaulon triquetrum* (Figure 49) grows in calcareous grasslands in Southwest Germany (Ahrens 2003). The upper layer of the substrate is colonized by rhizomes that branch and from which young shoots develop. This species is able to colonize the bare surfaces of the loess soil that is created by burrowing small mammals (and these rodents could contribute to dispersal by carrying rhizoids, rhizomes, propagules, and leaf fragments on their footpads and fur.



Figure 49. *Acaulon triquetrum*, a moss species that occupies bare soil created by burrowing rodents. Photo by Michael Lüth, with permission.

Another possibility is that plant fragments are carried in the gut and deposited at a different location. The first question to arise here is whether they are viable after their adventure in the gut. John Hribljan (unpublished) cultured microtine rodent scat from Isle Royale, Michigan, and

several fragments germinated (Figure 50) to produce new plants.



Figure 50. Culture of *Funaria hygrometrica* derived from feces collected from moss from Alaska. The size of the feces suggests these were microtine rodents. Photo by John Hribljan, with permission.

Beavers (*Castor canadensis*; Figure 51) are not known to use mosses, but they are ecological engineers that can change whole habitats. Their disturbance is often instrumental in the creation of wetlands (Adams 1993; Ponomarenko & Ponomarenko 2003). Such disturbances often result in the invasion of bryophytes and graminoids from wetlands into upland habitats (Ponomarenko & Ponomarenko 2003).



Figure 51. *Castor canadensis* – beaver – an engineer that creates wetlands. Photo by MSR, through Creative Commons.

Rodent Cycles

Rodent cycles have puzzled biologists for many decades (Turchin *et al.* 2000). The cycles were once understood to be 3-4 years, but now we understand that they are not so simple (Hansson 2002). They are characterized by lag phases and may be resource-driven. But lag phases can also be caused by predator effects. These drivers can force the population to spread to

suboptimal patches. Hansson reports that some rodents appear to be limited by food, especially mosses. The mosses recover slowly from overgrazing and are further limited by temperature.

Rodents can be responsible for considerable changes in the abundance of bryophytes (Rydgren *et al.* 2007). Early reports on increases in the bryophyte annual production and abundance suggest that climate change provides more favorable conditions (Økland 1997; Økland *et al.* 2004; Knorre *et al.* 2006). But more recently data suggest that in the boreal forests, rodent cycles impact the feather moss *Hylocomium splendens* (Figure 15). When rodents have long cycles, their peak years have the greatest impact, causing the greatest reduction in growth of the moss. The role of bryophytes in these ecosystems is typically as a food source (Hansson 1969; Tast 1991; Bondrup-Nielsen 1993), although bryophytes can also provide cover and nesting material. Further impact on moss persistence results from trampling (Rydgren *et al.* 2007). Runways open the carpet due to removal of tissue (Kalela & Koponen 1971; Ericson 1977). Furthermore, species such as *Brachythecium starkei* (Figure 38) and *Ceratodon purpureus* (Figure 35) rapidly colonize runways in the first year. Summer foraging on the shoot apex does not have a severe effect on the mosses, but winter grazing can exterminate a species clone, as seen in species of *Dicranum* (Figure 12-Figure 14, Figure 16) (Ericson 1977).

In Norway, fluctuations in rodent populations have profound impact on the success of the moss *Hylocomium splendens* (Figure 15) (Rydgren *et al.* 2007). The moss has its highest growth rate when the rodents are acyclic and becomes reduced when the periodicity and severity of the peak disturbance by rodents increases. Even its means of reproduction changes, with mature segments surviving in less variable environments, and regeneration from older branches responding to more variable environments. Rodent herbivory and trampling contribute to fragmentation from the mosses.

Such regeneration from older parts makes the population less fit than survival of mature stems (Rydgren *et al.* 2007). This is because large segments will survive for decades, but fragmentation results in small segments. These, in turn, have lower branching frequencies and lower probability of survival. Because of their small size, bryophytes such as *Hylocomium splendens* (Figure 15) may be able to use only two of the three resistance mechanisms known to tracheophytes (defense, escape, tolerance), lacking the size and lignin needed for physical defense against trampling and fragmentation. Rather, they seem to rely on tolerance through compensatory growth, greater photosynthesis, reallocation of resources, and activation of the meristem (Boege & Marquis 2005). The latter is triggered by damage to the apex that removes apical dominance, a phenomenon well known among many dicots.

For *Hylocomium splendens* (Figure 21), and many other large boreal mosses, reproduction by spores is rare, and growing tips provide the major form of reproduction (Økland 1995; Rydgren & Økland 2002; Cronberg *et al.* 2006). Fragmentation contributes to the diaspore bank, but there is a delay in growth, if it is successful at all (Rydgren *et al.* 2007). Nevertheless, it requires a severe impact of

30% loss of growing points and 15% loss of segments to reduce the population to a no-gain state under favorable growing conditions. Thus, with rodent cycles of 3-5 years and disturbance severities of only 15-30%, *Hylocomium splendens* (Figure 15) will survive.

Scenarios of climate effects on the microtine rodent cycles suggest that those cycles may change to become more irregular (Rydgren *et al.* 2007). Specifically studying the responses of the boreal moss *Hylocomium splendens* (Figure 15), Rydgren and coworkers found that the growth rates are higher in the acyclic scenarios, but that the population growth rates are progressively reduced when peak disturbance severities increase. When the environment is less variable, the mature segment of *H. splendens* (Figure 21) is the primary contributor to population growth rate. In a more variable environment, regeneration from branches of older parts becomes more important, a process that leads to reduced population fitness. Hence, if the cycles break down, abundance of *H. splendens* and other large bryophytes in boreal forests such as those of Norway will increase.

Snowbed bryophytes seem to be particularly vulnerable to rodents, perhaps because these sites are covered predominately by bryophytes. Moen *et al.* (1993) found that lemmings in northern Norway reduced the cover of graminoids by 33% and of mosses by 66% during the winter population peak. They considered this to be an important impact that helped to explain the snowbed vegetation dynamics.

As is usual in ecology, nothing operates alone. And the effects of large herbivores such as sheep can affect the impact of rodents on bryophytes, particularly in alpine ecosystems (Austrheim *et al.* 2007). Using exclosures, Austrheim and coworkers kept sheep out, but permitted access to rodents. This resulted in a significant increase in the grass *Deschampsia flexuosa* (Figure 52) within the exclosures. Frequencies of graminoids, herbs, and dwarf shrubs did not change in response to grazing, but of the 15 bryophyte species, cover of six bryophyte species groups changed, with three increasing and three decreasing significantly.

In their exclosure experiments, Austrheim *et al.* (2007) lumped bryophytes that were difficult to distinguish in the field to avoid taxonomic errors. Those that decreased in the exclosures were the *Plagiothecium* group [*P. nemorale* (Figure 53), *P. denticulatum* (Figure 18), *P. laetum* (Figure 54)] and the *Brachythecium* group [*B. reflexum* (Figure 55), *B. salebrosum* (Figure 56), *B. starkei* (Figure 38)], whereas *Straminergon stramineum* (Figure 57), *Pohlia nutans* (Figure 37), and *Cephalozia bicuspidata* (Figure 58) increased in the exclosures. At the same time, *Polytrichum* [*P. commune* (Figure 19), *Polytrichastrum formosum* (Figure 59), *P. longisetum* (Figure 60), *P. alpinum* (Figure 61)] increased in the grazed plots, whereas the leafy liverwort *Neoorthocaulis floerkei* (Figure 62) decreased in these grazed plots. The moss *Pleurozium schreberi* (Figure 8) and leafy liverwort *Ptilidium ciliare* (Figure 40) tended to increase in exclosures.



Figure 52. *Deschampsia flexuosa*, a grass that increased in exclosures that keep out sheep but permit an increase in rodent numbers. Photo by Miguel Porto, through Creative Commons.



Figure 53. *Plagiothecium nemorale*, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.



Figure 54. *Plagiothecium laetum*, a species that decreases in exclosures in alpine regions. Photo by Christian Peters, with permission.



Figure 55. *Brachythecium reflexum*, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.



Figure 56. *Brachythecium salebrosum*, a species that decreases in exclosures in alpine regions. Photo by Michael Lüth, with permission.



Figure 57. *Straminergon stramineum*, a species that increases in exclosures in alpine regions. Photo by David Holyoak, with permission.



Figure 58. *Cephalozia bicuspidata*, a short-lived colonizer, with perianths. Photo by Hermann Schachner Wikimedia Commons.



Figure 59. *Polytrichastrum formosum*, a species that increases in exclosures in alpine regions. Photo by David T. Holyoak, with permission.



Figure 60. *Polytrichastrum longisetum*, a species that increases in exclosures in alpine regions. Photo by Michael Lüth, with permission.



Figure 61. *Polytrichastrum alpinum*, a species that increases in exclosures in alpine regions. Photo by David Holyoak, with permission.



Figure 62. *Neoorthocaulis* (=Barbilophozia) *floerkei*, a species that is reduced in frequency by sheep. Photo by Janice Glime.

It was successional bryophytes that increased, along with the preferred fodder grass *Deschampsia flexuosa* (Figure 52) (Austrheim *et al.* 2007). The net result, however, was that neither tracheophyte nor bryophyte species richness was affected, nor was the total cover of either. It is interesting that when the sheep were excluded from grazing, the level of rodent grazing also diminished.

Austrheim and coworkers (2007) suggested four potential contributing factors for the changes in the bryophyte communities:

1. Exclusion of sheep reduces typical disturbance-favored pleurocarpous species such as the *Brachythecium* (Figure 38) and *Plagiothecium* (Figure 18, Figure 53-Figure 54) species groups.
2. Frequency of short-lived colonizers such as *Pohlia nutans* (Figure 37) and *Cephalozia bicuspidata* (Figure 58) increases.
3. Grazing favors grazing-resistant *Polytrichum* group species (Figure 19-Figure 20) (Helle & Aspi 1983; Väre *et al.* 1996; Virtanen 2000; Olofsson *et al.* 2004).

4. Herbivores cause a decrease in frequency of the leafy liverworts *Barbilophozia lycopodioides* (Figure 41) (sheep & rodents) and *Neoorthocaulis* (syn. = *Barbilophozia*) *floerkei* (Figure 62) (sheep).

Bryophyte recovery can influence the structure of the rodent cycle. In their comparison of rodent cycling at Barrow, Alaska, USA, with that of North Fennoscandian lemmings, Oksanen *et al.* (2008) considered that the contrasting population fluctuations between these two areas probably depended on the different growth rates of the mosses. Based on data from Barrow, Turchin and Batzli (2001) assumed that it would take only two years for a complete recovery of mosses, based on the data from the wet tundra there (Tieszen *et al.* 1980). However, in North Fennoscandian habitats where lemmings over-winter, recovery from grazing requires at least ten years (Oksanen 1983).

Dispersal

Feces created by the rodents have the potential to provide a means of dispersal. Vole digestion time varies considerably, depending on the diet (Lee & Houston 1993). Nevertheless, voles have a very efficient digestion for plants. This high efficiency in the digestion of vegetal matter may lie in their habit of **coprophagy**. That is, they consume their own feces and cycle their food through their digestive system a second time. Seed diets can take considerably longer than leaf diets. But how long does it take for a moss diet to traverse the gut?

Whatever the residence time, feces of rodents may be deposited in their habitat, including among the local bryophytes, but also along runways or on other soil. If the rodent fails to re-ingest these feces, the moss provides a suitable habitat for germination, and the rodent may carry it some distance to a new location. Hribljan (unpublished data) provides support for this possibility; mosses germinated from feces collected from among mosses in Alaska (Figure 63).

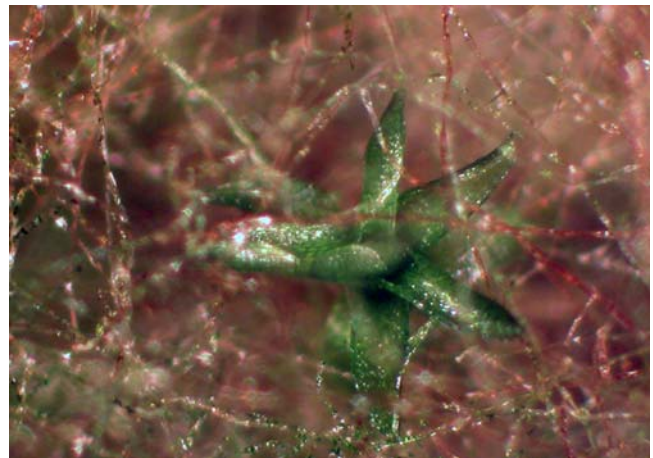


Figure 63. Developing *Funaria hygrometrica* from a culture of rodent feces collected from moss in Alaska. Photo by John Hribljan, with permission.

The experimental evidence of bryophyte dispersal by rodents is limited. Kimmerer and Young (1996) examined the effect of gap size and regeneration niche on the

coexistence of bryophyte species. Based on their study on two epixylic mosses, *Tetraphis pellucida* (Figure 64-Figure 65) and *Dicranum flagellare* (Figure 66), rodents appear to play a major role in both dispersal and distribution. Their activity creates gaps that *Dicranum flagellare* can colonize on the tops of logs. *Tetraphis pellucida* occurs primarily on the vertical surfaces at the sides of the logs. Both species produce propagules that can adhere to the rodents.



Figure 64. *Tetraphis pellucida*, a species that lives on vertical surfaces of logs and is dispersed by rodents. Photo by Jan-Peter Frahm, with permission.



Figure 65. *Tetraphis pellucida* gemma, the dispersal unit carried by rodents. Photo by UBC Botany Website, with permission.

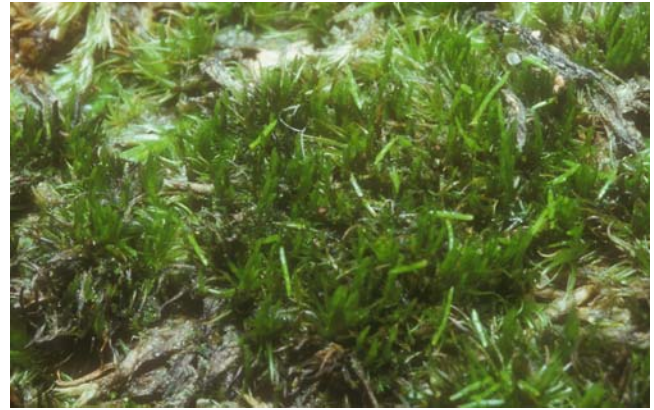


Figure 66. *Dicranum flagellare* with brood branches, many of which are broken off and lying on the moss in this image. Photo by Janice Glime.

Muroidea – Hamsters, Voles, Lemmings, and New World Rats and Mice

Muridae – Mice, etc.

This is the largest family of rodents and the largest of mammals (Wikipedia 2016). Although the family name is derived from the Latin *mus*, meaning mouse, it also includes some kinds of voles, rats, and others. None is native to North America, but a number of species have arrived here, presumably with humans.

Micromys minutus – Eurasian Harvest Mouse

The Eurasian Harvest Mouse (*Micromys minutus*; Figure 67-Figure 69) has a wide distribution in the temperate and humid climate zone of East Asia and western Europe (Harris & Trout 1991). In urban environments, the habitat may differ, but Dickman (1986) found that even in such a setting fecal pellets can contain small amounts of moss.



Figure 67. *Micromys minutus*, Eurasian harvest mouse, a mouse that consumes mosses. Photo by Bj. Schoenmakers, through Creative Commons.



Figure 68. *Micromys minutus* constructing a nest. Photo by Hajotthu, through Creative Commons.



Figure 69. Completed summer nest of *Micromys minutus*. Photo by Alexis Martin, through Creative Commons.

Myodes = Clethrionomys – Red-backed Voles

It seems that there is no agreement among systematists as to the preferred generic group name for these voles. I have chosen to use *Myodes*, but with nothing more than convenience to back up my choice. Furthermore, rodents with the common name of vole are in both the **Muridae** and the **Cricetidae** (covered in the next subchapter).

Longton (1992) states that mosses are "freely consumed" by Arctic and alpine voles. Voles seem to at times make important uses of mosses. In her messages to Bryonet on 3 December 2004 and 12 January 2008, Kate Frego described some of the relationships of the voles to bryophytes. She reported that they clipped the *Dicranum polysetum* (Figure 13) they had earlier avoided as food. Frego states that this is only anecdotal data, but she observed quite extensive "clipped" pathways of *Dicranum polysetum* as the snow melted, with some areas resembling "rooms" with nests, others with copious mouse droppings.

In the sub-nivean tunnels that they made, they had trimmed off all the moss tips into neat, compact carpets!

Mosses are able to offer other advantages to both the rodents and their food plants. The moss layer provides a temperature stabilizing factor (Fuller *et al.* 1969). The temperature lag is greater in the moss than in the layer under the snow. Furthermore, when snow melts and refreezes, the structure of the snow changes, causing a sharp increase in its thermal conductivity. Hence, the snow layer experiences wide temperature fluctuations, whereas these are considerably damped in the moss layer (Figure 70).

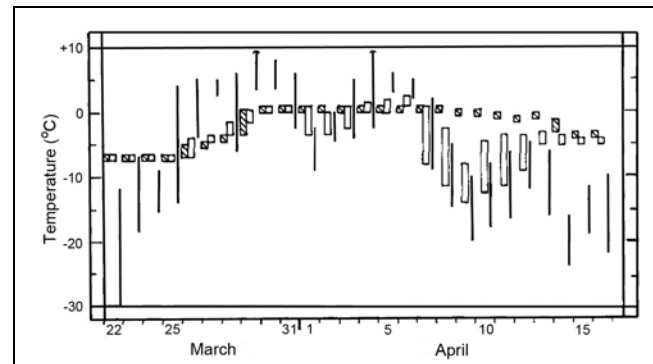


Figure 70. Daily moss (cross-hatched box), snow 5 cm above moss (open box), and air temperatures (vertical line). Beginning 1 April, physical structure of the snow was changing. Redrawn from Fuller *et al.* 1969.

In the Alaskan Arctic tundra, experiments in which mosses were removed demonstrated that *Sphagnum* (Figure 42) removal permitted an increase in the shrub *Betula nana* (Figure 71) (Gough *et al.* 2007). Hence, vole activity could change the vegetation patterns in these Arctic systems. Unfortunately, Gough *et al.* (2007) did not have any data on the relationship of *Sphagnum* to vole activity.



Figure 71. *Betula nana*, a shrub that benefits when a rodent damages the *Sphagnum*. Photo by Foledman, through Creative Commons.

The diet of *Myodes* differs among species, but also differs within species among habitats (Hansson 1985). For example, *Myodes glareolus* (Figure 24) feeds mostly on seeds in the deciduous forest and on fungal tissues in coniferous forests.

***Myodes rufocanus* – Grey Red-backed Vole**

The grey red-backed vole (*Myodes rufocanus*; Figure 23) extends through a large range in the northern Palearctic from northern Fennoscandia through northern Russia, and northeastern and northern Korea and the islands of Sakhalin (Russia), and Japan (Abe *et al.* 2005), then far south to northern parts of Mongolia and China (Wilson & Reeder 2005).

Myodes rufocanus (Figure 23) is often common in areas where Norwegian lemmings (*Lemmus lemmus*; Figure 28) reside, but unlike the lemmings, the voles do not usually eat the mosses, preferring blueberry plants (*Vaccinium myrtillus*; Figure 72) and other dicots instead (Kalela 1957; Virtanen *et al.* 1997). This separation of diets keeps them from competing for food in this food-limited environment.



Figure 72. *Vaccinium myrtillus*, common food of *Myodes rufocanus*, the grey red-backed vole. Photo by Anneli Salo, through Creative Commons.

The summer nest of *Myodes rufocanus* is constructed of grass, leaves, lichens, and moss (Chester 2016).

***Myodes rutilus* – Northern Red-backed Vole**

The northern red-backed vole (*Myodes rutilus*; Figure 73) is distributed in the northern Holarctic, including northern Fennoscandia, European Russia, Siberia, north Xinjiang Province in China, through Mongolia, to northeast China and northern parts of the Korean peninsula, the islands of Sakhalin (Russia), Hokkaido (Japan), Alaska (USA), and Canada (Linzey *et al.* 2016). It lives in the subarctic birch forest zone and in northern parts of the boreal forest zone. Its greatest abundance is in productive (eutrophic or mesotrophic) forests, with a dense understory of grasses, herbs, or moss. It prefers mature old-growth forests, but, unlike other *Myodes* species, it is absent from clear-felled areas. It is herbivorous, eating green parts of grasses and herbaceous plants, nuts, seeds, bark, lichen, fungus, and insects, storing food for winter. In the autumn it stores seeds.



Figure 73. *Myodes rutilus*, a species that lives in mossy spruce forests. Photo by Zbyszek Boratynski, through Creative Commons.

The habitat of the northern red-backed vole (*Myodes rutilus*; Figure 73) can change with seasons. In the Daisetsu Mountains of Japan, the vole was captured in areas with dense cover of the bamboo *Sasa* and a thin cover of mosses in July (Onoyama 1989). However, in September it showed a preference for dense tree cover.

In Alaska, West (1977) found a seasonal difference in the dispersion pattern of the northern red-backed vole. In summer, they lacked any pattern of aggregation. During midwinter they had moved to just one section of the trapping grid. In early spring, they once more dispersed with no pattern of aggregation. When West analyzed the vegetation structure, he found that the area of winter aggregation had a significantly thicker moss layer than the areas used in the summer. West considered this to indicate that the aggregation was the result of a limited area of suitable moss cover for overwintering.

The food of *Myodes rutilus* (Figure 73) is primarily seeds from dwarf shrubs and forbs, lichens, and above and belowground fungi (West 1982). I found no evidence that the voles eat bryophytes, so it is likely that the mosses serve to provide space for moving around between the snow and the frozen ground.

***Myodes gapperi* – Southern Red-backed Vole**

The southern red-backed vole (*Myodes gapperi*; Figure 74) is also known as *Clethrionomys gapperi*, living in Canada and the northern United States (Wikipedia 2017b). Pivorum and Bunch (2005) stated that its ideal habitat would be mesic with an abundance of litter, rotting logs, moss-covered rocks, exposed roots, and rock crevices. It often is restricted to mossy habitats (Headstrom 1970). It may burrow beneath *Sphagnum* (Figure 42) to make its nest, concealing it from view (Headstrom 1970). In peatlands it uses moss, among other bits of vegetation, to line the nest (Linzey & Brecht 2002).

In these peatlands and elsewhere it uses natural runways among the mosses, roots, and rocks (Linzey & Brecht 2002). *Myodes gapperi* (Figure 74) uses runways in warm weather, but tunnels through the snow in winter (Wikipedia 2017b). In New Jersey, USA, the red-backed vole lives only in *Sphagnum* peatlands of the pine barrens, where during winter, the moss is often frozen, necessitating using food gathered earlier for its winter supply (Stone & Cram 1902).



Figure 74. *Myodes gapperi*, southern red-backed vole, with *Sphagnum*. Photo by Phil Myers, through Creative Commons.

In humid forests it often occurs among mossy rocks (Komarek & Komarek 1938). Craig *et al.* (2014) hinted at the possibility that mosses may contribute to needed cover in areas with limited or no downed wood. It is the most abundant mammal among the tundra vegetation on Mt. Washington, New Hampshire, USA, where it lives among mosses, rocks, and dwarf willows. In a study comparing this species with *Peromyscus keenii* (mice) in Alaska, the southern red-backed vole preferred habitats with more moss cover than that of *P. keenii* (Smith *et al.* 2005). In fact, the growth of the young mice is inversely correlated to the percent cover of mosses on the forest floor. But in spring, even the voles have a negative correlation with moss, perhaps due to those sites being wetter.

Hodson *et al.* (2010) found that the southern red-backed voles responded to moisture availability. When moss cover was low, the voles had either reduced maximum potential fitness or an increased relative rate of decline of fitness with density. This species has high water requirements (Getz 1968) and generally occurs in mesic forests with moist microclimates and moss cover (Morris 1996; Orrock *et al.* 2000). The most abundant mosses in their habitats were *Pleurozium schreberi* (Figure 8), *Ptilium crista-castrensis* (Figure 11), and *Sphagnum* spp. (Figure 42). Hodson and coworkers (2010) found that in cut vs uncut forest stands, moss cover was the most important parameter in determining success of *Myodes gapperi* (Figure 74). They did not determine if the moss was essential, but rather it could be that the moss also occurred in the most moist habitats.

The red-backed voles (*Myodes* spp.) are both omnivorous and opportunistic, with a diet that changes with the seasons and availability (Boonstra & Krebs 2012). In North America in spring and late fall, they mainly feed on dicot leaves. In summer and fall they eat seeds, berries, fruits, and insects. Throughout the year they also include monocots, mosses, and lichens (Perrin 1979; Vickery 1979; Merritt & Merritt 1978; Merritt 1981; Martell 1981).

Côté *et al.* (2003) reported 3% or more bryophytes in the gut of *Myodes gapperi* (Figure 74) in a black spruce

(*Picea mariana*; Figure 75) forest. In a study in West Virginia, USA, small amounts of moss were retrieved from a few red-backed vole stomachs, but these never formed a major food source (Schloyer 1977). Maser and Maser (1988) emphasized that lichens were particularly important in winter in the Cascade Mountains of North America. However, these become depleted under the snow, forcing the voles to eat vascular plants and mosses. This is especially important because these voles do not hibernate, but are active year-round.



Figure 75. *Picea mariana* forest and bog, Lake County, Minnesota, USA. Photo by Jason J. Husveth, with online permission.

Myodes glareolus – Bank Vole

The bank vole, known by *Myodes glareolus* (Figure 76) and *Clethrionomys glareolus* (depending on your perspective), occurs from Europe through Central Asia (Jonsson *et al.* 2000; Macdonald 2001). This species builds its nest in a hole under the ground, but spends much of the day active above ground (EOL 2017a).



Figure 76. *Myodes glareolus* peering out of a tree hole. Photo by Johan Dierckx Nature Diary.

In Poland, *Myodes glareolus* (Figure 76) was present in live and snap traps in *Sphagnum* (Figure 42) peat bogs and were predominant in that type of trapping (Cienchanowski *et al.* 2012). Torre and Arrizabalaga (2008) determined the habitat preferences of *Myodes glareolus* in a Mediterranean mountain range. They found that mosses accounted for far more (90%) of the variance than other measured environmental parameters. The bank voles preferred moist habitats where mosses were more abundant. But were the mosses important to them, or was it that the same habitat suited both the mosses and the bank voles? This is a recurring question with the voles and needs to be experimentally tested.

Myodes glareolus (Figure 76) does not appear to eat mosses as a regular diet component, but it is a herbivore, eating leaves of woody plants, soft fruits and seeds, and leaf litter (in winter) (Watts 1968). The mosses do occasionally enter consumption (Figure 77), perhaps because it is an easier means to get the seeds or the springtime arthropods when they are present among the mosses. Bank voles in northern Sweden consumed mosses at a frequency of about 20% of their diet (Hansson 1979), suggesting that habitat, and perhaps latitude, may influence diet choices.



Figure 77. *Myodes glareolus*, bank vole eating mosses in the Netherlands. Photo by Andrew Spink, with permission.

In European forests, the bank vole is the dominant small rodent species (Hansson 1983). It uses the moss *Mnium hornum* (Figure 44) for winter cover, as well as odd decaying logs (Kikkawa 1964). In these habitats, it consumes small amounts of moss, but bark is its primary food, especially in some winters (Hansson 1983). Gębczyńska (1976) likewise found mosses in gut analyses, being present in 30% of the vole stomachs in spring in an oak hornbeam forest. Nevertheless, vegetative parts of plants and insects comprised the major portion of the diet.

Apodemus sylvaticus – Wood Mouse

The ubiquitous wood mouse, *Apodemus sylvaticus* (Figure 78), is distributed throughout Europe (with the exception of Finland and northern parts of Scandinavia, the Baltic, and Russia) and parts of North Africa (Schlitter 2016). It uses mosses, leaves, and grass to construct its nest (Duke 2011). In Berkshire, UK, winter cover is provided by the moss *Mnium hornum* (Figure 44) (Kikkawa 1964). The wood mouse does not appear to eat

mosses as a regular diet component, but rather is a seed eater (Watts 1968). The mosses do occasionally enter consumption, perhaps because it is an easier means to get the seeds and the springtime arthropods when they are present among the mosses.



Figure 78. *Apodemus sylvaticus*, wood mouse, a species that uses mosses in its nest. Photo by Mick E. Talbot, through Creative Commons.

Pseudohydromys and *Mirzamys* – Moss Mice

These little-known genera have several species in the mossy forests of New Guinea (Helgen & Helgen 2009). I have been unable to find out why these are called moss mice. Perhaps it is because many of the species live in mossy forests. Likewise, little is known of their biology. We can only infer that mosses have some importance in the choice of habitat by some species. These moss-dwelling Papua New Guinea species include *Pseudohydromys eleanorae*, *P. murinus*, and *P. ellermani* in mossy montane forest; *P. occidentalis* (Indonesia and Papua New Guinea) and *P. fuscus* in mossy mid and upper montane forest; *P. musseri* in mossy upper montane forest (Helgen & Helgen 2009; Helgen & Wright 2017).

The related genus *Mirzamys* likewise is known from mossy upper montane forests in New Guinea (Helgen & Helgen 2009). *Mirzamys louiseae* occurs here and *M. norahae* lives in mossy rainforest habitats that can be characterized as elfin or upper montane forest.

Otomys sloggetti – Sloggett's Vlei Rat

The Sloggett's Vlei Rat (*Otomys sloggetti*; Figure 79) occurs typically in habitats with xeric soils and rocky outcrops of South Africa, but Lynch (1992) found it to be in large numbers in a mesic bog with no rocky outcrops. In the bog habitat, it was a burrower, occupying an extensive burrow system. The young are born during the warm wet months of October to March.



Figure 79. *Otomys sloggetti*, a species that lives in boggy habitats. Photo by Terry Rosenmeier, through Creative Commons.

The boggy habitats are characterized by numerous hummocks about 20 cm high and 30 cm in diameter. Lynch (1992) suggested that these were originally formed by burrowing by *Cryptomys hottentotus* (Figure 48). Then the *O. sloggetti* (Figure 79) enlarged and cleaned the tunnels. These excavated areas are colonized by various tracheophytes, especially dwarf sedges, and mosses. The activity of the voles adds soil to the top, creating the hummock landscape. Others consider the hummocks to originate from freeze-thaw activity and not by the rodent activity.

***Rattus rattus* – Black Rat**

The black rat (*Rattus rattus*; Figure 80) has travelled with humans, earning it the alternative name of ship rat. As a result of this human association, it is known from all continents (EOL 2017b).



Figure 80. *Rattus rattus*, black rat, in tree in New Zealand, a species that includes mosses in its varied diet. Photo by James Russell, with permission.

The diet of the black rat is almost as varied as its distribution. Clout (1980) found that in a *Pinus radiata* plantation it consumed invertebrates, fungi, and plant material, including mosses and pine needle fragments. Unlike many of the voles, no seeds or fruits were eaten.

Tobin *et al.* (1994) found seasonal changes in the diet of rats in a Hawaiian macadamia orchard. Mosses occurred in 48% of the rat stomachs, with a mean of 4% of the diet. The moss *Sematophyllum caespitosum* was a ubiquitous moss there on branches and tree trunks.

Summary

Rodents can have major impacts on the bryophyte communities, especially in the Arctic. Many rodents have mosses in the gut and feces, but these often seem to be the result of accidental intake. Nevertheless, some rodents seem to include bryophytes as an important part of the diet, often increasing the percentage of intake in winter. Researchers have suggested that this switch may be a need for nitrogen, arachidonic acid, or fiber. In other cases, it may be a simple matter of availability. A number of **Microtine** rodents consume mosses in the winter, even though the mosses are poorly digested, being high in fiber, and providing little nitrogen or digestible energy, but often the nutrient content in the Arctic is superior or differs little from that of tracheophytes in the region.

The shoot tips seem most desirable for food, but in winter the moss may be clipped at the bottom. Some records indicate that moss capsules are also eaten. Such grazing in northern habitats can have severe impacts on the moss communities, as indicated by exclosures. A 1-year time lag between feeding and the evidence of bryophyte species changes is common. Weft and other large species can benefit from regeneration from rhizomes and dispersal of fragments or propagules.

Many rodents use mosses in the construction of nests, particularly as part of the lining. In bogs, several species may coexist in a single bog, some using them for food or to make nests, tunnels, or runways.

Bryophytes are impacted by the rodents in multiple ways. Negative impacts include diminished cover and competition from flowering plants. But at other times they may benefit through exposed soil and removal of taller grasses. The rodents can also serve as dispersal agents, and runways open new habitats where colonizers can grow, increasing diversity.

Moss users in the **Muridae** include *Micromys minutus* (minor food), *Myodes rufocanus* (among nest materials), *M. rutilus* (aggregate in mosses in winter), *M. gapperi* (mossy habitats, minor food), *M. glareolus* (mossy habitats, winter cover, minor food), *Apodemus sylvaticus* (minor food, winter cover), *Pseudohydromys* (mossy rainforest), *Mirzamys* (mossy rainforest), *Otomys sloggetti* (makes hummocks in bogs), and *Rattus rattus* (minor food).

Acknowledgments

This chapter has benefitted greatly from anecdotal records sent to me by bryologists and friends who observed these small rodents interacting with mosses in the field. Kate Frego has provided invaluable anecdotal experience to me.

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CHAPTER 17-2

RODENTS – MUROIDEA: NON-MURIDAE

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CHAPTER 17-2

RODENTS – MUROIDEA: NON-MURIDAE



Figure 1. This exposed runway of the heather vole (*Phenacomys intermedius/ungava*) shows the clippings of mosses and barren nature of their path. According to Kate Frego, this appearance is common when the snow melts in the spring. Photo courtesy of Kate Frego.

Cricetidae – Hamsters, Voles, Lemmings, and New World Rats and Mice

The voles, lemmings, and muskrats are known as the microtine rodents, the **Microtinae**. This subfamily comprises the largest numbers among the **Rodentia** in the Northern Hemisphere. They are distinguished by their molar teeth, which have prismatic cusps in the shape of alternating triangles. These sharp teeth are suitable for grinding and are an adaptation to the herbivorous diet. Batzli and Jung (1980) demonstrated that microtine rodents near Atkasook, Alaska, eat mosses.

Chionomys nivalis – Snow Vole

The snow vole (*Chionomys nivalis*; Figure 2) is distributed from southern Europe to the Near and Middle East (Castiglia *et al.* 2009), extending to the Caucasus, Turkey, Israel, Lebanon, Syria, and Iran (Shenbrot & Krasnov 2005). The European populations are restricted to

rocky and mountainous areas at mostly higher elevations (Castiglia *et al.* 2009).



Figure 2. *Chionomys nivalis*, a species that may suffer from heavy metal toxicity by eating bryophytes and lichens. Photo by Svičková, through Creative Commons.

Janiga *et al.* (2016) reminded us of the role mosses could play in consumption of lead and other pollutants by this and other microtine species. The concentrations of Pb, Cd, Zn, and S in mosses from the Alps revealed rising levels with altitude, despite the scarcity of pollutants at higher elevations (Zechmeister 1995; Šoltés 1998). These pollutants seem to have arrived with the precipitation through long-distance transport. Several researchers have suggested that mosses (and lichens) may have a significant influence on the lead concentrations in *Chionomys nivalis* (Figure 2) (Sivertsen *et al.* 1995; Belcheva *et al.* 1998; Metcheva *et al.* 2008; Janiga *et al.* 2012). Janiga and coworkers considered this to be a special problem due to winter consumption of mosses.

***Microtus agrestis* – Field Vole**

The field vole (*Microtus agrestis*; Figure 3) is a widespread European Palaearctic species, ranging from western Europe eastwards through Russia to Lake Baikal in south-east Siberia.



Figure 3. *Microtus agrestis* among mosses. Photo from Wikimedia Commons.

It is not just in the Arctic that rodents eat mosses. Ferns (1976) found that *Microtus agrestis* (Figure 3) eats both mosses and liverworts in a larch plantation in Great Britain. The mosses comprised 20% of the area of materials in the feces (scat) under the microscope. *Microtus agrestis* exhibits seasonal differences in diet. Grasses are the primary food, with the greatest consumption rate in winter (Faber & Ma 1986). Herbs and mosses are also important, especially in spring and summer. Considerable variability occurs in the diet, depending on the kind of habitat and time of year. The moss *Hypnum cupressiforme* (Figure 4) forms an important part of the diet, but it is interesting that it seems not to be consumed in winter.

In a study of small rodents in Scandinavia, Hansson (1971) demonstrated the need of more water by herbivores than that needed by granivores. This can explain their choice of mossy habitats and may even explain their consumption of the mosses.

Microtus agrestis (Figure 3) in Fennoscandia exhibits population cycles (Turchin & Hanski 2001). Many researchers have attempted to model these cycles, but causes are still controversial. Turchin and Hanski concluded that their evidence supports the predation hypothesis. Many models have considered food to be the

driving factor, but Turchin and Hanski considered this to hold only in systems like the moss-eating lemmings. Nevertheless, a disappearance of mosses due to consumption, runways under snow, or fires could make the habitat unsuitable for these small, moisture-dependent rodents.



Figure 4. *Hypnum cupressiforme* var *cupressiforme*, an important food for *Microtus agrestis*. Photo by David Holyoak, with permission.

Like *Chionomys nivalis* (Figure 2), *Microtus agrestis* (Figure 3) are subject to consumption of heavy metals that have become incorporated into their food items (Ma *et al.* 1991). And these can enter their bodies with mosses as the carrier. Fortunately, *Microtus agrestis* consumes only small amounts of *Hypnum cupressiforme* (Figure 4) in these areas, a moss known to contain considerably more lead and cadmium than the flowering plants in the diet.

***Microtus pennsylvanicus* – Meadow Vole**

The meadow vole (*Microtus pennsylvanicus*; Figure 5) is the North American counterpart of *M. agrestis* (Figure 3). It occurs throughout most of Canada and Alaska, USA, south through the northern half of the United States, to Oregon, northern Utah, central New Mexico, Kansas, northern Missouri, Georgia, and South Carolina; it is disjunct (by 500 km) in Florida, USA, and Chihuahua, Mexico (Hall 1981; Cassola 2016a).



Figure 5. *Microtus pennsylvanicus*, a species that makes paths among mosses. Photo by John White, with permission.

These voles occupy a wide variety of habitats, ranging from dry pastures and wooded swamps to marshes and orchards (Cassola 2016a). The soil needs to be loose and organic to permit tunneling. Their underground tunnels are extensive. In Wisconsin, Getz (1970) found that the meadow vole inhabits areas that have a dense, spongy mat comprised of several moss species. The voles make paths among these mosses, but the paths do not have the character of distinct runways.

The meadow vole seems to prefer introduced species over native ones for its food (Thompson 1965), perhaps indicative of its European ancestors. When given 30 plant species choices from a variety of habitats, eight of the top ten chosen foods were introduced species. By contrast, the native boreal plants and bog plants occupied the last eight positions of preference. Peat moss (*Sphagnum*; Figure 6) was scarcely touched.



Figure 6. *Sphagnum capillifolium*, in a genus among the least preferred among the 30 plants provided to *Microtus pennsylvanicus* as food choices. Photo by David Holyoak, with permission.

Kate Frego relates that during her summer PhD research in the boreal forest of northern Ontario, Canada, she observed both red-backed voles (*Myodes*) and meadow voles (*Microtus pennsylvanicus*; Figure 5) eating moss shoots, tips first. "I did a little test with the meadow voles (which are placid enough to sit on my hand and eat!), and offered them choices which I ranked. I have to say it was a small sample size, 4 voles as I recall, but they were very consistent! They seemed to 'prefer' *Ptilium crista-castrensis* (Figure 7), and *Pleurozium schreberi* (Figure 8), would occasionally take *Ptilidium ciliare* (Figure 9), and politely declined all the *Dicranum* spp. I had at hand [*D. polysetum* (Figure 10) and *D. scoparium* (Figure 11)]. Unfortunately, I have no info on whether the munched vegetative bits survived passage through their guts. (I actually have photos of one meadow vole scoffing down a *Ptilium* shoot)."



Figure 7. *Ptilium crista-castrensis*, a moss eaten by *Phenacomys intermedius*. Photo by Janice Glime.



Figure 8. *Pleurozium schreberi*, a moss eaten by *Phenacomys intermedius*. Photo by Janice Glime.

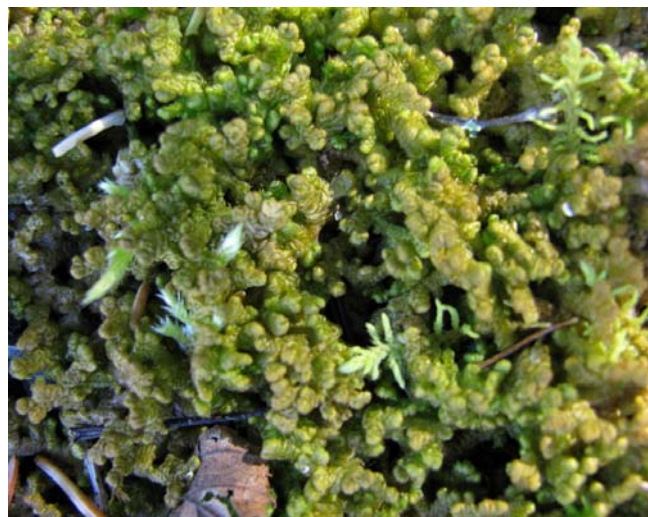


Figure 9. *Ptilidium ciliare*, a leafy liverwort eaten by *Phenacomys intermedius*. Photo by Janice Glime.



Figure 10. *Dicranum polysetum*, a moss eaten by *Phenacomys intermedius*. Photo by Janice Glime.



Figure 11. *Dicranum scoparium*, one of the preferred forest mosses for the wood lemming. Photo by Janice Glime.

Linzey (1984) cautioned that estimates of mosses in fecal samples of this and other rodents may be overestimates of the diet percentage because they, along with monocots, have poor digestibility (Batzli & Pitelka 1971), giving them over-representation. Linzey found that mosses were only eaten by *Microtus pennsylvanicus* in winter, whereas Frego observed them eating mosses in summer.

***Microtus oeconomus* – Tundra Vole**

The tundra vole, *Microtus oeconomus* (Figure 12), has the northernmost distribution of any of the North American species of *Microtus*, and is common also in the northern parts of Eurasia (known there as root voles) (EOL 2017a). Although the habitat preference is moist meadows near water, the tundra vole can also inhabit *Sphagnum* bogs (Figure 13) (Ciechanowski *et al.* 2012).

Alaskan populations of the tundra vole consume mosses, but these comprise less than 10% of the diet (Batzli & Jung 1980). Batzli and Jung (1980) suggested that grazing pressure by the tundra voles may be competitive with both the brown lemmings (*Lemmus sibiricus*; Figure 14) and collared lemmings (*Dicrostonyx torquatus*) because of overlapping food niches, thus restricting the distribution of the voles through competition with lemmings.



Figure 12. *Microtus oeconomus*, a species that can be found in *Sphagnum* bogs. Photo by аймаина хикари, through Creative Commons.



Figure 13. *Picea mariana* forest with *Sphagnum*, Lake County, MN. Photo by Jason J. Husveth, with online permission.



Figure 14. *Lemmus sibiricus*, a potential competitor for food with *Dicrostonyx torquatus*. Photo by Ansgar Walk, through Creative Commons.

***Microtus pinetorum* – Pine Vole, Woodland Vole**

The woodland vole (*Microtus pinetorum*; Figure 15) is distributed from extreme southern Ontario, Canada, and throughout the eastern United States with the exception of peninsular Florida and the coastal plains of the southeastern

states; there is a disjunct population in Texas (Cassola 2016b). The rock vole (*Microtus chrotorrhinus*; Figure 16) and the woodland vole (*Microtus pinetorum*) both live where there are rocks, mosses, ferns, and forbs in North America (Kirkland & Knipe 1979; Christian & Daniels 1985; Merritt 1987). This relationship suggests that these voles may depend on the bryophytes, but detailed studies seem still to be needed.



Figure 15. *Microtus pinetorum*, a woodland vole that lives in habitats with bryophytes and uses them in nesting and runways. Photo by Phil Myers, through Creative Commons.

Pine voles (*Microtus pinetorum*; Figure 15) use bryophytes for nest sites and runways (Rhodes & Richmond 1985). Given the choice of mixed loam with peat moss (3:1 vol/vol), base mixture with added gravel (3:2 v/v), or (1:1 v/v), the moles chose the loam/peat moss mixture for subsurface tunnels and nests over the other choices. In fact, they always avoided the soil/stone mix. One reason for their choice of mossy habitats may be their need for temperatures below 30°C (Rhodes & Richmond 1985). I would expect dark soil to heat more readily than moist, aerated mosses. We need data to support this, however, because we also know that mosses easily reach temperatures higher than that of air, especially at the surface (Nørgaard 1951; Hribljan & Glime, unpublished data). On the other hand, the sub-surface temperature can experience a much smaller diurnal temperature range (Nørgaard 1951).

Microtus xanthognathus – Taiga Vole

The taiga vole (*Microtus xanthognathus*) inhabits northwestern Canada to Alaska (Wikipedia 2017). It lives in forested habitats near streams, lakes, or bogs. Its runways are a combination of underground and surface runways (EOL 2017c). These voles construct communal nests and food caches in August and September. The nests are made of dry grasses and are located ~15-20 cm underground. The food supply must be reached through the nest. The taiga voles huddle together in groups of 5-10 individuals, keeping each other warm and sharing the food during winter. The life span is short, as in most other voles. The young voles are born in the summer and breed the next summer. They do not survive the following winter.

The taiga vole (*Microtus xanthognathus*) requires an abundant supply of rhizomes for winter food (Wolff & Lidicker 1980; Conroy & Cook 1999). In summer it feeds on horsetails, grasses, and berries. But mosses provide it with ground cover and are a necessary part of its habitat.

Microtus chrotorrhinus – Rock Vole

The rock vole (*Microtus chrotorrhinus*; Figure 16) is distributed in Canada from Labrador through the Gaspé Peninsula, New Brunswick, west to Ontario, and in the USA from northeastern Minnesota southward at higher elevations to New England, New York, and northeastern Pennsylvania, and disjunctly in the southern Appalachians to Virginia, western North Carolina, and eastern Tennessee (Kirkland & Jannett 1982; Handley & Pagels 1991).



Figure 16. *Microtus chrotorrhinus*, a species that is most abundant in moist mossy areas. Photo by Roger W. Barbour, Smithsonian Institutes, with online permission.

The rock vole in Virginia, USA, lives in sites with abundant vegetation, mosses, talus- and rock-laden slopes, typical of the habitats for this species (Orrock *et al.* 1999). In contrast to these rocky sites, in Labrador and other areas they are most common in moist mossy areas near streams and ponds, thick brush, and open-canopy forests (Buech *et al.* 1977; Kirkland & Knipe 1979; Kirkland & Jannett 1982; Lansing 2005).

Orrock and Pagels (2003) found that more mosses were present in yellow birch and other forests with rock voles than those without these rodents. The ability of mosses to ameliorate the effects of air temperature may contribute to their preference for mossy habitats (Fuller *et al.* 1969). Kirkland and Jannett (1982) considered the moss cover of yellow birch and rock vole sites to be indicative of the cool, moist microclimate there, but suggested that the mosses also may serve as a reserve food source.

One rock vole (*Microtus chrotorrhinus*; Figure 16) in New York, USA, was actually snap-trapped with the moss *Atrichum undulatum* (Figure 17) in its mouth! (Whitaker & Martin 1977). The stomach also contained the same moss in a relatively unchewed state. Among those voles examined, leafy portions of *A. undulatum* comprised 5.2% of the stomach contents.



Figure 17. *Atrichum undulatum*, a moss that forms part of the diet of *Microtus chrotorrhinus*. Photo by Brian Eversham, with permission.

These voles also pull clumps of *Sphagnum* (Figure 6) for building their nests (Martin 1971), which are lined with grass and have multiple entrance tunnels (North Carolina GAP Analysis Project 2005). In the Appalachian and Adirondack Mountains of eastern North America, this species occurs in small populations that live among large, moss-covered rock fragments (Kilpatrick & Crowell 1985).

***Phenacomys intermedius* – Western Heather Vole**

Phenacomys intermedius was once considered to include the eastern North America populations, but some authors have separated the eastern populations into *Phenacomys ungava* (Cassola 2016c). Nevertheless, some consider *P. ungava* to be only a subspecies. Since it is not always clear which species is included in the study, I will use *Phenacomys intermedius/ungava* to designate my uncertainty.

The distribution of the western heather vole (*Phenacomys intermedius*; Figure 18) extends across northern Canada from Labrador to the Yukon Territory and in the USA from the western mainland south to New Mexico (Banfield 1974; Fitzgerald *et al.* 1994). It is active both night and day.

Kate Frego (Bryonet) relays her experience with heather voles in northern Ontario, Canada: "In the summer, while trying to photograph a Heather Vole (in my hand; Figure 18), I tickled its nose with a sprig of moss, and was stunned when it grabbed the moss and ate the whole sprig."



Figure 18. *Phenacomys intermedius/ungava*, eastern heather vole. Photo courtesy of Kate Frego.

The western heather vole (*Phenacomys intermedius*; Figure 18) lives in mountains in the areas near or above **timberline** (altitude at which trees cease to grow into actual trees; treeline; Figure 19) (EOL 2017d). Their food is typically leaves, seeds, berries, and bark of willow and other shrubs. Their summer nests are underground, but winter nests occur at ground level next to a bush, rock, or stump. Their nests are comprised of twigs, leaves, and grass. Males are territorially aggressive during mating season, but in winter they may nest together to maintain warmth.



Figure 19. Treeline on mountain over Firth River in Ivvavik National Park, YT. Photo by Daniel Case, through Creative Commons.

In Minnesota, USA, the heather vole (*Phenacomys intermedius/ungava*; Figure 18) occurs in a wide range of habitats. These include open pine and spruce forests with an understory of heath, shrubby vegetation, and moist, mossy meadows (Banfield 1974; Christian 1999). These locations are not above timberline, but winters are long, cold, and snowy.

It appears that the connection of heather voles with mosses may be accidental in some cases, at least in some cases. Côté *et al.* (2003) reported that *Phenacomys intermedius/ungava* in a black spruce forest in eastern Canada had 3% or more bryophytes among the material retrieved from the gut. Other observations demonstrate that this species does indeed eat mosses (Glime 1996). It was caught in the act grabbing and nibbling the moss *Ptilium crista-castrensis* (Figure 7), from tip down to base. This vole also ate *Pleurozium schreberi* (Figure 8) and *Ptilidium ciliare* (Figure 9). On the other hand, it rejected *Dicranum polysetum* (Figure 10). The winter runways, constructed at the ground surface under the snow, were conspicuous after snowmelt by the closely clipped *Dicranum* with its clippings lying nearby (Figure 1).

***Phenacomys ungava* – Eastern Heather Vole**

The eastern heather vole (*Phenacomys ungava*; Figure 20-Figure 21) is widely distributed across Canada, but its populations seem to be sparse (EOL 2017e), partly due to its avoidance of traps. Recently most authors consider it to be part of the species *P. intermedius* (Figure 18) (Cassola 2016c). It seems to avoid traps, making it hard to estimate the population sizes (EOL 2017e). These voles often pile their food near their burrows at night,

making it accessible for daytime food. They don't hibernate, and their winter food source is unknown. Nevertheless, they clip mosses in their runways (Figure 22), potentially dispersing them to other locations.



Figure 20. *Phenacomys ungava*, a species that uses mosses in its nests. Photo by Gerda Nordquist, MN DNR.



Figure 21. *Phenacomys intermedius/ungava*, heather vole, a species that clips *Dicranum* (Figure 10) species in winter and is known to eat other boreal bryophytes. Photo courtesy of Kate Frego.



Figure 22. Close view of heather vole runway in May, showing moss clippings. Photo courtesy of Kate Frego.

Phenacomys ungava (Figure 20-Figure 21) constructs its nests just below the ground surface, using grass, moss, and other materials (Foster 1961). Braun *et al.* (2013) described the summer nests similarly as constructed of soft materials, including grass, moss, leaves, and plant down.

Its habits are poorly known because of the difficulty of trapping it and of keeping it alive.

***Arborimus albipes* – White-footed Vole**

The white-footed vole (*Arborimus albipes*; Figure 23) lives in trees in dense forests of the Pacific Northwest of North America, seldom seeing direct sunshine through the canopy (Jewett 1920). They commonly live near rivers or streams (EOL 2017f). Their home is on the moss-covered forest floor (Jewett 1920). Their burrows have never been observed, but their claws suggest that they are adapted for burrowing (EOL 2017f). They are active year-round.



Figure 23. *Arborimus albipes*, white-footed vole, an inhabitant of moss-covered forests. Photo by Michael Durham, through Creative Commons.

The abundant mosses in their native forests provide them with some of their food; seeds, fruits, fungi, and animals were absent among their ingested material (Verts & Carraway 1995).

***Arborimus longicaudus* – Red Tree Vole**

The red tree vole (*Arborimus longicaudus*; Figure 24) is another native of the Pacific Northwest (Manning & Maguire 1999). It is likely that *Arborimus longicaudus* is not a committed moss user. It eats conifer needles. Nevertheless, the nests (see discarded resin ducts in Figure 25) can contain mosses (Biswell *et al.* 2017). "From the ground, red tree vole nests generally appear as dark haphazard accumulations of twigs, needles, moss, and/or lichens on the topside of a large branch or whorl of branches against the bole of a tree." Some are known to nest under the mosses that cover large branches of old trees (Carey, in Wilson & Ruff 1999).



Figure 24. *Arborimus longicaudus*, red tree vole, in a spruce tree. This species includes mosses among its nesting materials. Photo by Stephen DeStefano, through public domain.



Figure 25. Discarded resin ducts from Douglas fir, discards from nest-making activity of *Arborimus longicaudus* (tree vole). Photo by Petrelharp, through Creative Commons.

***Peromyscus maniculatus* – Deer Mouse**

Deer mice (*Peromyscus maniculatus*; Figure 26) are the most widespread of the North American rodents (EOL 2017g), extending from the northern treeline in Alaska and Canada southward to central Mexico, but absent in the eastern United States (Baker *et al.* 1983). They likewise have a wide range of habitats, occupying almost every kind of habitat available (EOL 2017g). They can easily climb, tunnel through snow, or run about on the surface. Nests in this species are typically located in dead trees, under logs and stumps, or among mosses (Sharpe & Millar 1991). Their association with humans includes nesting in such human creations as mattresses (EOL 2017g).



Figure 26. *Peromyscus maniculatus* in a spruce tree. Photo by Phil Myers, through Creative Commons.

I opened my email one day to find a delightful story unfolding from a former undergraduate student of mine, Steve Juntikka. A fat little mouse, which was later identified as *Peromyscus maniculatus* (Figure 27), on Isle Royale was busily consuming capsules from the moss *Funaria hygrometrica* (Figure 28). Isle Royale National Park is the largest island in Lake Superior on the border of USA and Canada. The mice most likely arrived as stowaways.



Figure 27. Juvenile *Peromyscus maniculatus* on Isle Royale, Michigan, devouring capsules of *Funaria hygrometrica*. Photo courtesy of Steve Juntikka.



Figure 28. *Funaria hygrometrica* one day after the mouse dined on it, showing the orange tips of setae where capsules have been removed. Photo courtesy of Steve Juntikka.

Juntikka described the lurching behavior of the mouse (Figure 27), "Looks like the capsules were the best tasting and you have never seen those little whiskers move so fast. I could not believe the front feet moving with a doggy paddle motion to rake in the capsules. The hind legs were spread apart to balance the weight while each capsule disappeared with delight." The next day there weren't many capsules left (Figure 28).

Like most of the rodents, deer mouse populations fluctuate, typically 3-5 years, and this seems at times to be correlated with food availability (EOL 2017g). Deer mice are night active, feeding opportunistically on seeds, nuts, fruits, berries, insects, and other animal matter, as well as any human food scraps they find.

Bryophytes are not a major part of the diet, but Côté *et al.* (2003) found that the gut contained 3% or more mosses

in their black spruce habitat. The diet changes between juveniles and adults (Van Horne 1982). In a coniferous forest, the adults consumed more hard-bodied insects than did juveniles. They ate few monocots, including grasses, concentrating on dicots and ferns, but a few mosses were eaten.

***Neotoma cinerea* – Bushy-tailed Woodrat**

The bushy-tailed woodrats (*Neotoma cinerea*; Figure 29) extend from the Yukon Territory and Northwest Territories of Canada south to Arizona and New Mexico, USA, and from California east to the Badlands in South Dakota (EOL 2017h). They are very territorial, with both males and females marking their territories with a musky scent and white color on rock ridges. They pile vegetation and other collected items, making middens of a conspicuous size. These are not mere temporary constructions, but edifices on which the animals may defecate or urinate. When the middens bake in the sun, they become as hard as rocks and can last for tens of thousands of years!



Figure 29. *Neotoma cinerea*, a species that uses dry mosses and grasses in its nests. Photo by Ken Cole, USGS, through public domain.

Based on observations in five localities, Brown (1968) found that the nests themselves must be dry, relatively dark, and create inaccessibility to would-be predators (Figure 30). The portion constructed by the woodrat is often an open, cup-shaped nest composed of dry mosses and grass.



Figure 30. *Neotoma* sp., Packrat, midden in Nevada, USA. Photo by Toiyabe, through Creative Commons.

Foraging occurs at long distances from the nest, up to 470 m for females (Topping & Millar 1996). Topping and Millar suggested that this long distance may be related to availability of appropriate food. This nighttime activity is affected by the brightness of moonlight, most likely avoiding the increased predation in bright moonlight as they cross open areas to reach foraging areas with greater cover (Topping *et al.* 1999). Morton and Pereyra (2008) verified nighttime haying behavior of these rodents in Wisconsin, USA, where they gathered mostly poisonous flowering plants. They found that the food plants were cut and stacked to dry before they were placed within the dens, possibly decreasing the toxicity.

***Neotoma fuscipes* – Dusky-footed Woodrat**

The dusky-footed wood rat (*Neotoma fuscipes*; Figure 31) lives in the extreme western United States, from the Columbia River in western Oregon south to the inner Coastal Range of west-central California, and the north Sierra Nevadas, east-central California (EOL 2017k). It typically lives in woods that have a dense understory. Even though they are very small, they build large (up to 1 m in diameter and height), elaborate houses made of sticks (Figure 32). These may be located on the ground, in the tree canopy, on rocky slopes, or even in abandoned buildings. These "houses" typically include several nesting and resting chambers as well as several used for storing food and "treasures" collected from among human creations. English (1923) reported that this species uses mosses to line compartments of its nests, keeping them clean and well kept. The toilet may be within the house or outside it (EOL 2017k). Although the woodrats are solitary, these houses may be used successively by a number of woodrats. Mosses do not seem to be part of the diet.



Figure 31. *Neotoma fuscipes*, a species that uses mosses to line its nests. Picture by Mbmceach, through Creative Commons.



Figure 32. *Neotoma fuscipes* nest. Photo by Donna Pomeroy, through Creative Commons.

***Neotoma magister* – Allegheny Woodrat**

The Allegheny woodrat (*Neotoma magister*; Figure 33), an endangered species (Mengak 2002), is the only woodrat in the Appalachian Mountain range in eastern USA (EOL 2017j). The species is able to occupy a wide range of macrohabitat conditions (Castleberry *et al.* 2002). On the other hand, it chooses its habitat based on conditions of the microhabitat. Castleberry and coworkers suggested that this selection may relate to the high mobility of the species and its herbivore diet.



Figure 33. *Neotoma magister*, a species that ingests a small amount of moss. Photo by Alan Cressler, through Creative Commons.

The Allegheny woodrat forages only at night, consuming primarily fruits, nuts, seeds, leaves, and fungi (EOL 2017j). Castleberry *et al.* (2002) found that the diet typically had more than 2% moss in the Allegheny Plateau of West Virginia and Virginia, USA. There are no studies to indicate if this is digested, or if it simply comes along with seeds and fungi found among the moss stems.

***Lemmus* – Lemmings**

Lemmings (*Lemmus*) are well known moss consumers, in addition to sedges and grasses (Batzli 1993). The story of the importance of mosses to their survival has been evolving over the many years of my career.

Ever since Walt Disney filmed lemmings plunging over cliffs into the ocean during mass migrations, lemmings have gotten the reputation of being suicidal. But rumors claim that the suicidal tendency is mere fiction and that the Disney crew drove the lemmings off with helicopters.

Mosses may actually help to explain the Disney film that shows lemmings committing suicide (Ekerholm *et al.* 2001). It is doubtful that they really have any intention of committing suicide, but lemmings do tend to eat themselves literally out of house and home during the winter, then become fully exposed when the snow melts. That means they must scurry to a new location for both food and shelter. And sometimes they **might** scurry too far and reach the fiords where they **could** plummet to the ocean and be unable to climb the steep cliffs to safety. But there seems to be no scientific documentation that they actually do plummet to their deaths (Turchin *et al.* 2000). In fact, Ekerholm *et al.* (2001) contend that those lemmings that do not "jump the cliff" are actually the ones that commit suicide.

It was 1924 when Charles Elton reported that lemming populations reach the maximum density their environment permits, remain there until their predators catch up, then crash because the predator overeats. But Turchin *et al.* (2000) claim this is not true for lemmings, although it is true for voles. We do know, however, that lemmings cycle through mass migrations as a result of overpopulation that depletes their habitat. And Turchin and coworkers (2000) claim that it is the absence of mosses that triggers this moving carpet of furry bodies. Foraging on mosses on the rocky tundra, lemmings soon remove these slow-growing plants faster than the mosses can re-grow, say Turchin and coworkers. Hence, they are forced to move elsewhere or starve. Unfortunately, many fail to negotiate the dangers and energy required to cross rivers and lakes, ultimately drowning and adding credence to the Disney story.

In a 20-year study in northern Norway, Ekerholm and colleagues (2001) found a "vague" 10-year cycle for the highland lemmings. This cycle corresponds with the time required for snowbed mosses to recover from their grazing and reach a 100 g m⁻² biomass (Kyllönen & Laine 1980; Oksanen 1983). Furthermore, the crashes in lemming populations correspond to times of massive destruction of the highland mosses (Oksanen & Oksanen 1981; Moen *et al.* 1993; Ekerholm *et al.* 2001). In some areas, the lemming population can recover using grassy habitats, but in the more northern areas, recovery of mosses is necessary before a real "outbreak" of lemmings can occur (Ekerholm *et al.* 2001).

Batzli (1983), in reviewing the responses of Arctic lemmings to nutritional factors, concluded that the availability of high quality forage drives the differences in densities of the Arctic rodents between habitats and in different seasons. But in addition to nutritional quality, fluctuations in plant secondary compounds may also play a major role. The Norwegian lemming (*Lemmus lemmus*; Figure 34) continues to eat monocots in winter, but it increases its intake of mosses (Koshkina 1962; Batzli & Pitelka 1983), even though the monocots are more digestible than the mosses (Batzli & Cole 1979). As Prins (1982a) suggested, perhaps it was the secondary compound arachidonic acid that made mosses desirable, especially in preparation and duration of winter, by providing better protection against the cold.



Figure 34. *Lemmus lemmus*, the Norwegian lemming, a species that supplements its winter diet by increasing moss consumption. Photo by Argus Fin, through Creative Commons.

Turchin *et al.* (2000) questioned whether it was prey or predation that controlled lemming numbers. As predators, these rodents eat mosses, especially in winter. The lemmings (*Lemmus*; Figure 34, Figure 43) can destroy ~90% of the moss cover and cut off all the monocot shoots in their habitats (Batzli 1981), creating an open field where they must run to find food. The mosses regrow slowly, leaving the lemmings exposed when the snow melts, particularly in large populations (Turchin *et al.* 2000). This causes the predators to have a particularly easy time finding and catching the lemmings as prey. The extra food results in an increase in the predator population (Snowy Owl and others) resulting from highly successful reproduction. The Snowy Owls are strong fliers. When the lemming population subsequently crashes from the owl predation, the owls are able to migrate to other areas where prey is sufficiently abundant (Line 1997). Using graphic models of the population dynamics, Turchin and coworkers (2000) concluded that the various rodent cycles are not due to a single mechanism, making a universal explanation unlikely.

Based on the low amounts of digestible energy that lemmings appear to derive from mosses, Prins (1982a) suggested that lemmings and other vertebrates of cold climates eat mosses for reasons other than nutrition. He hypothesized that ingestion of a highly unsaturated fatty acid, arachidonic acid, may be an adaptive mechanism that helps protect against low temperatures, making the footpads more pliable. Animals do not synthesize arachidonic acid and its concentration in mosses (up to 35 % of fatty acids) is the highest reported in plants.

In addition to the leaves and stems of mosses, high Arctic lemmings also consume the capsules of mosses (Catherine La Farge, Bryonet 15 January 2008); the mosses have often been decapitated (Catherine La Farge, Bryonet 30 March 2016). Little is known about the secondary compounds of capsules, particularly with regard to seasonal changes in them.

In addition to gut analyses, flattened moss beds, and observations of lemmings eating mosses, habitat choice supports the importance of mosses in the life of a lemming (Oksanen 1983). The sites where lemmings (*Lemmus* sp.; Figure 34) were observed have five times as much moss meadow as sites where lemmings did not visit. Following the population crash of the lemmings, there was an 8.4-fold increase in the moss biomass.

Lemmings have the disadvantage of being attacked from above. They are the main food of the Snowy Owl (*Bubo scandiacus*; Figure 35), a powerful bird with a 1.5 m wingspan (Line 1997). The lemmings protect themselves in summer by living in shallow burrows or under lichen-covered rocks. However, in winter these same lemmings curl up in balls of grasses and mosses under the snow and ice. They create a maze of tunnels and emerge only to feed on buds, twigs, and bark of the dwarf tundra shrubs. It is on these feeding forays that the Snowy Owl is able to catch them for food. An adult Snowy owl will eat 3-5 lemmings per day; a pair of owls with its brood will consume 1900 to 2,600 lemmings in the period of May to September. Their breeding success is tied to years when the lemmings are numerous.



Figure 35. The Snowy Owl, *Bubo scandiacus*, male, a major lemming predator. Photo by Michael Gäbler, through Creative Commons.

In addition to the effects of harvesting mosses for food, lemmings affect the bryophyte diversity of their Arctic habitats through the construction of runways and burrows. Lemming runways and burrows provide openings in the tundra that provide some bryophyte species with the reduced competition they need. Among these are *Bryum wrightii* (Figure 36), *Desmatodon leucostoma* (Figure 37), and *Funaria polaris* (Steere 1976).



Figure 36. *Bryum wrightii*, a species that colonizes lemming runways and burrow openings. Photo by Jean Faubert, with permission.



Figure 37. *Desmatodon leucostoma*, a species that colonizes lemming runways and burrow openings. Photo by Jonathon Sleath, BBS website, with permission.

Dale Vitt (pers. comm. January 2018) has shared his lemming experiences with me. On the Canadian Arctic Devon Island (Figure 38-Figure 39), he found that both *Funaria polaris* and *F. microstoma* (Figure 40) grew on the openings to lemming burrows (Figure 41).



Figure 38. Truelove Lowlands, Devon Island. Photo by Martin Brummell, through Creative Commons.



Figure 39. Devon Island showing permafrost. Photo Anthonaes, through Creative Commons.



Figure 40. *Funaria microstoma*, a moss found at the openings of lemming burrows in the Arctic. Photo courtesy of Dale Vitt.



Figure 41. Lemming burrow on Devon Island showing bryophytes at entrance of the burrow. Photo courtesy of Dale Vitt.

Although some lemmings partition their niches by having different diets, there can be considerable overlap. Soininen *et al.* (2015) used DNA metabarcoding of feces to demonstrate diet overlap among high Arctic lemmings in the winter. Contrasting to previous analyses, they found that *Salix* dominated the diets of both collared lemmings (*Dicrostonyx groenlandicus*) and brown lemmings (*Lemmus trimucronatus*) on Bylot Island, whereas mosses were a relatively minor contribution. *Salix* is abundant on the island, and feeding by the two lemming species has little impact on its cover. Despite the paucity of bryophytes in the winter diet, Dominique Fauteux (pers. comm. January 2018) has observed the lemmings on Bylot Island eating *Polytrichum* and *Aulacomnium* heads "many, many times."

Gruyer *et al.* (2008) found, using exclosures (Figure 42)), that on Bylot Island the lemmings have little impact on plant biomass, even in peak years. This contrasts with the effects of other herbivores on the island.



Figure 42. Lemming enclosure 1x1 m on Bylot Island in 2014. Photo courtesy of Dominique Fauteux.

***Lemmus lemmus* – Norwegian Lemming)**

The Norwegian lemming (*Lemmus lemmus*; Figure 43) is the only **endemic** (not occurring outside a restricted area) vertebrate species in Fennoscandia (Tast 1991). It typically lives in the alpine tundra (Eurola *et al.* 1984), but may expand to forests during peak population years (Tast 1991). The species faces potential extinction as a result of climate warming. It is adapted for cold weather, and geography prevents it from moving to colder regions.



Figure 43. *Lemmus lemmus*, the Norwegian lemming, a moss eater. Photo through Creative Commons.

Norwegian lemmings reproduce year-round and often reproduce under snow (Tast 1991). They can have up to 100 offspring per pair in one year (EOL 2017k). The Norwegian lemmings consume mosses year round as their primary food item, including all habitats (Tast 1991; Turchin & Batzli 2001). Nevertheless, the proportion in the diet decreases toward the end of the main breeding season. When moss consumption again rises, breeding resumes. These mosses grow even in winter in the Arctic, providing fresh food all year.

At the highest population peaks, winter consumption by various lemming species can remove the growing portions of 90-100% of both mosses and graminoids (Thompson 1955; Pitelka 1957; Koshkina 1961; Schultz 1968; Kalela & Koponen 1971; Kiryuschenko 1979;

Henttonen & Jävinen 1981; Chernyavsky *et al.* 1981; Moen *et al.* 1993). In the Kilpisjärvi region, Finnish Lapland, no large invasion of *Lemmus lemmus* (Figure 43) occurred between 1971 and 1984, resulting in continuous increase in the bryophyte biomass (Eurola *et al.* 1984). Timo Koponen (Bryonet 13 January 2008) considered *Dicranum* (Figure 10) species essential for these lemmings to survive.

Further evidence of lemming-moss relationships comes from enclosure experiments in snowbeds at Kilpisjärvi in Finnish Lapland. Despite low lemming densities during the study period, Virtanen (2000) and coworkers (1997) found "profound" changes in an 8-year enclosure, with a three-times thicker cover of haircap mosses [Polytrichaceae: *Polytrichastrum alpinum* (Figure 44), *P. sexangulare* (Figure 45), *Polytrichum commune* (Figure 46), *P. hyperboreum* (Figure 47), *P. juniperinum* (Figure 48), *P. piliferum* (Figure 49)] and a few graminoids (Figure 50). After 15 years, polytrichaceous mosses in the enclosures had a large number of dead shoots and Virtanen (2000) suggested that they may actually depend on grazing for maintenance (Figure 50). Virtanen *et al.* (1997) suggested that polytrichaceous mosses had the advantage of a significant subterranean rhizome that permitted their survival during periods of heavy grazing. Outside the plots, one could find plants of low stature (Figure 50), including liverworts [*Cephalozia* spp. (Figure 51), *Gymnomitrium* spp. (Figure 52), *Moerckia blyttii* (Figure 53)] and the low moss *Kiaeria starkei* (Figure 54). *Kiaeria* was absent in the enclosures after 15 years (Virtanen 2000). It was only in the open that colonizing species such as *Pohlia nutans* (Figure 55) and *P. drummondii* (Figure 56) were present (Figure 50). Hence, the lemmings had a strong influence on the species composition of the moss communities. Thus, in this enclosure experiment in a mountain snowbed, the biomass of mosses increased within the enclosures during 5 years of experiments (Virtanen 2000).



Figure 44. *Polytrichastrum alpinum*, a species that can increase 3-fold when lemming herbivory is prevented. Photo by David Holyoak, with permission.



Figure 45. *Polytrichastrum sexangulare*, a species that can have 3X thicker cover in lemming exclosures. Photo by Hermann Schachner, through Creative Commons.



Figure 48. *Polytrichum juniperinum*, a species that can reach 3X thicker cover in lemming exclosures. Photo by Janice Glime.



Figure 46. *Polytrichum commune*, a species that can have 3X thicker cover in lemming exclosures. Photo by A. J. Silverside, with permission.



Figure 49. *Polytrichum piliferum*, a species that can reach 3X thicker cover in lemming exclosures. Photo by Li Zhang, with permission.



Figure 47. *Polytrichum hyperboreum* with capsules, a species that can reach 3X thicker cover in lemming exclosures. Photo by Michael Lüth, with permission.

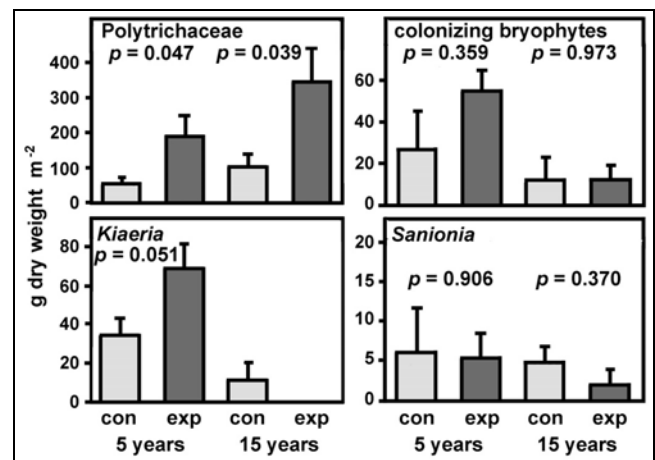


Figure 50. Effect of grazing exclosures (**exp**) compared to controls (**con**) on bryophytes in a lemming habitat at Kilpisjärvi in Finnish Lapland after five and fifteen years of exclosure from herbivory. Redrawn from Virtanen 2000.



Figure 51. The leafy liverwort, *Cephalozia bicuspidata*, with perianths, member of a genus that is able to grow outside the lemming exclosures. Photo by Hermann Schachner, through Wikimedia Commons.



Figure 52. *Gymnomitrium concinnatum*, member of a genus that is able to grow outside the lemming exclosures. Photo by Hermann Schachner, through Creative Commons.



Figure 53. *Moerckia blyttii*, a species that is able to grow outside the lemming exclosures. Photo by Michael Lüth, with permission.



Figure 54. *Kiaeria starkei*, a moss that completely disappears in lemming exclosures after 15 years. Photo by Michael Lüth, with permission.



Figure 55. *Pohlia nutans*, a colonizing species, in the Khibiny Mountains, Apatity, Murmansk. Photo by Michael Lüth, with permission.



Figure 56. *Pohlia drummondii* with bulbils, a colonizing species, that occupies open areas. Photo by David T. Holyoak, with permission.

Do lemmings control the mosses, or do mosses control the lemmings? Oksanen (1983) found five times as much moss on a site visited by lemmings (*Lemmus* sp.; Figure 57) as found at a site they did not visit. But it appears that it was in fact a two-way control; after a population crash at Kilpisjarvi, Finland, there was an 8.4-fold increase in moss biomass on the site the lemmings had grazed. When the

moss "dies," lemmings leave or die. When lemmings leave, mosses rebound.

Ims *et al.* (2008) considered the suggestion that Norwegian lemmings (*Lemmus lemmus*; Figure 57) are especially sensitive to winter climatic conditions. They reasoned that this may be due to their reliance on mosses. These low plants exist at the base of the snow collection and are probably locked in ice when adhering water refreezes after a melt, making periods of time when even this food is unavailable. Hence, warmer climates where freezing and thawing are common throughout the winter may be unfavorable because of food unavailability.

The Norwegian lemming (*Lemmus lemmus*; Figure 57) in forest tundra eats more mosses than the less available grasses and sedges (Koshkina 1961), and the Nearctic brown lemming (*Lemmus trimucronatus*; Figure 58), a species of circumpolar tundra, eats more mosses in winter when monocots are least available (Batzli 1975).



Figure 57. *Lemmus lemmus*, the Norwegian lemming, a species that devours mosses in the tundra. Photo by Andreaze, through Creative Commons.



Figure 58. *Lemmus trimucronatus*, the Nearctic brown lemming, a species that increases its moss consumption in winter. Image from EOL, through Creative Commons.

One should expect that grazing would change the structure of the bryophyte community, but in fact, the predicted changes did not occur on the Arctic islands studied (Virtanen 2000). *Sanionia uncinata* (Figure 59) is common on Arctic islands lacking grazers, but in the 15 years of enclosure experiments it remained a subordinate species in both enclosures and non-enclosures. Furthermore, the expected change in colonizing species – small liverworts and *Pohlia* spp. (Figure 55-Figure 56)

(Oksanen & Ranta 1992) did not occur in either treatment (Virtanen 2000).



Figure 59. *Sanionia uncinata*, a species that is common when grazers are absent, but that was only a subordinate species after 15 years in enclosures. Photo by Michael Lüth, with permission.

In some locations, the Norwegian lemming (*Lemmus lemmus*; Figure 34, Figure 43, Figure 57), along with reindeer, can have a profound effect on bryophyte vegetation. They eat the competing graminoids, resulting in more space for bryophytes to obtain sufficient sunlight. In enclosure experiments, Virtanen (2000) showed that mosses such as *Kiaeria* (Figure 54) were reduced to low biomass or total absence after 15 years of exclusion of these herbivores. The *Polytrichaceae* (Figure 44-Figure 49) still dominated the habitat, but its litter had increased. But in the shorter experiment of only five years, mosses increased, no doubt due to the absence of winter feeding by lemmings. This suggests that the 4-5-year cycles of lemmings in many areas may be in tune with the growth rate of the bryophytes, affording them sufficient recovery time. Virtanen concluded that even in such a low productivity environment as the Norwegian Arctic, herbivory has a major impact in controlling the ecosystem, a system where mosses and lichens are typically the dominant vegetation.

Another study in the Fennoscandian mountain range of northernmost Sweden and Norway likewise demonstrated that Norwegian lemmings (*Lemmus lemmus*; Figure 57) can have a significant impact on the vegetation (Olofsson *et al.* 2004). Both *Dicranum* (Figure 10) and *Polytrichum* (Figure 46-Figure 49) species increased significantly in the enclosures. These are preferred winter forage for lemmings (Kalela 1961). The liverwort *Ptilidium ciliare* (Figure 9), on the other hand, became greatly reduced when herbivory disappeared in the enclosures. Liverworts are known to be weak competitors that benefit from grazing (on competing plants) and disturbance (Gjaerevoll 1956; Moen *et al.* 1993; Virtanen *et al.* 1997); presumably, grazing on the surrounding plants provided the *P. ciliare* with the exposure it needed.

Not only do the lemmings reduce the mosses by foraging, but they also use them in nests. The Norwegian lemming builds a dry nest lined with mosses and lichens, then includes mosses as the bulk of its diet (Anonymous 2005). A moss population crash occurs when the lemmings exhaust the moss flora, which regrows slowly, leaving the

lemmings to seek new locations to forage (Turchin *et al.* 2000). Thus, lemmings can be seen running in large numbers in search of food and shelter.

We have seen that metal pollutants accumulated by mosses have been detrimental to populations of other small rodents. Kataev *et al.* (1994) further reported that the decline in *Lemmus lemmus* (Figure 43, Figure 57) in regions with high SO₂ and heavy metal emissions may be due to the decrease in abundance of mosses due to the pollution.

Apparently capsules also form part of the diet. Olga Belkina (pers. comm. 13 November 2012) observed *Oligotrichum hercynicum* (Figure 60) with setae but no capsules (Figure 61) in a Lapland State Nature Biosphere Reserve. Feces of *Lemmus lemmus* were nearby (Figure 62). On another occasion, her research team identified fragments of *Hylocomium splendens* (Figure 63) and *Sanionia uncinata* (Figure 59) in the gut. Kalela *et al.* (1961) found that the forest populations of the Norwegian lemming typically survives winter by eating *Pleurozium schreberi* (Figure 64) and *Hylocomium splendens*.



Figure 60. *Oligotrichum hercynicum* with capsules bitten by lemmings. Photo courtesy of Olga Belkina.



Figure 61. *Oligotrichum hercynicum* with capsules bitten by lemmings. Photo courtesy of Olga Belkina.



Figure 62. *Oligotrichum hercynicum* with capsules bitten by lemmings and scat that reminds us of their former presence. Photo courtesy of Olga Belkina.



Figure 63. *Hylocomium splendens*, winter staple food for the Norwegian lemming. Photo by Daniel Mosquin, Botany Website, UBC, with permission.



Figure 64. *Pleurozium schreberi*, winter staple food for the Norwegian lemming. Photo by Janice Glime.

Lemmus sibiricus/trimucronatus – Brown Lemmings

The brown lemming (*Lemmus sibiricus*; Figure 14) has been divided into subspecies, and the North American (Nearctic) portion of the species has been named as a separate species, *Lemmus trimucronatus* (Figure 58)

(Wilson & Reeder 2005); the Nearctic brown lemming, *Lemmus sibiricus* s.s. (black-footed lemming) is distributed in the Palearctic tundra zone from the White Sea to Kolyma (Russian Federation). Unfortunately, I have found no lemming studies mentioning mosses for the eastern Palearctic.

Brown lemmings near Barrow, Alaska, (presumably *Lemmus trimucronatus*; Figure 58) eat mosses, as well as grasses and sedges, in winter, and in drier habitats the mosses form up to 40% of the diet (Batzli & Pitelka 1983). When lemming numbers peak in their 4-6 year cycle, such mosses as *Calliergon* (Figure 65), *Dicranum* (Figure 10), and *Polytrichum* (Figure 46-Figure 49) species can form 5-20% of the diet in summer and 30-40% in winter (Bunnell *et al.* 1975). Lemmings actually prefer mosses (Chapin *et al.* 1986). Mosses show seasonal carbohydrate fluctuations, with a decline in brown tissues in summer and an increase in autumn. *Aulacomnium* (Figure 66) species show greater seasonal fluctuation of carbohydrate concentration in brown material than do *Polytrichum/Pogonatum/Polytrichastrum?* (Figure 44-Figure 49) species. Mosses have the highest concentrations of lignin-like materials, whereas *Eriophorum* (cottongrass; Figure 67) and lichens have the lowest. The preference ranking of the lemmings, who specialized on mosses and graminoids, correlate positively with fiber and negatively with mineral nutrient contents, suggesting that fiber may be important in the diet.



Figure 65. *Calliergon giganteum*, in a genus that forms up to 40% of the diet of the brown lemming in Alaska. Photo by A. Neumann, Biopix, through Creative Commons.



Figure 66. *Aulacomnium turgidum*, in a genus that shows large seasonal fluctuation of carbohydrates in brown material. Photo by Michael Lüth, with permission.



Figure 67. *Eriophorum vaginatum*, a genus with low concentrations of lignin-like materials. Photo by Roger D. Bull, through Creative Commons.

Schultz (1968) estimated that in their peak years, brown lemmings (*Lemmus sibiricus*; Figure 68) consume up to 90% of the primary production in their North American habitats; Batzli (1975) found the same 90% consumption in the low Arctic, where mosses and monocots were the primary winter food. In Scandinavia, Norwegian lemmings consume 66% of the mosses (Moen *et al.* 1993).



Figure 68. *Lemmus sibiricus*, a species that eats mostly mosses and grasses in winter. Photo by Ansgar Walk, through Creative Commons.

In northern Alaska, *Lemmus trimucronatus* (Figure 58) specializes on monocots and mosses, whereas the other small rodents eat primarily flowering plants (Batzli & Jung 1980; Batzli 1983). *Lemmus trimucronatus* continues consuming monocots in the winter, leaving behind the basal 1 cm and permitting regrowth. However, their moss consumption increases (Koshkina 1962; Batzli & Pitelka 1983; Batzli 1983; Rodgers 1990; Turchin & Batzli 2001), reaching up to 40% of the diet (Batzli & Pitelka 1983). Batzli (1983) determined that mosses are the least digestible group for the rodents (Batzli & Cole 1979), providing much less energy. Nevertheless, they can be up to 40% of the diet in drier habitats, where they are more important than in moist habitats (Batzli & Pitelka 1983). Batzli (1983) reasoned that instead they must provide a nutrient supplement. On the other hand, Rodgers (1990) suggests that when graminoids become senescent at the end

of summer, the lemmings are forced to eat a greater proportion of mosses. In cafeteria-style experiments, lemmings that had been fed artificial diets chose mosses in the same proportion as those individuals that had been raised on a natural diet, indicating the choice of mosses was genetically based (Rodgers & Lewis 1985). Food choice indicated that preference was based primarily on macronutrients and caloric content. Habitat made no difference in diet choices (Rodgers & Lewis 1986).

Nevertheless, the Alaskan brown lemmings (*Lemmus trimucronatus*; Figure 58) cannot survive and reproduce on a diet exclusively of mosses. It appears that in Barrow, Alaska, USA, the summer digestibility is poor and the consumption by these lemmings is low (Batzli & Cole 1979). But in winter, if densities are medium to high (~>30 lemmings per hectare), they rapidly exhaust the graminoids and must live on a diet of 100% mosses (Turchin & Batzli 2001).

With the low digestibility of mosses (Batzli & Cole 1979), it is not surprising that captive Nearctic brown lemmings (*Lemmus trimucronatus*; Figure 58) lost weight on a moss-only diet, supporting the suggestion that mosses must serve some function other than as a source of energy. Batzli and Cole (1979) suggest that the high concentrations of calcium, magnesium, and iron may be beneficial.

In a feeding experiment using *Funaria hygrometrica* (Figure 28), the lemmings of Devon Island ate only the capsules (Pakarinen & Vitt 1974). Pakarinen and Vitt suggested that the choice of capsules may have been related to the high lipid content of the spores. The availability of the highly polyunsaturated fatty acid arachidonic acid (Gellerman *et al.* 1972) almost exclusively in mosses (and also *Equisetum*) may be especially important to these small mammals that must run about on and under the snow (Prins 1982b). Northern climates seem to increase the predation on mosses, perhaps because the arachidonic acids might help to keep the fats in the foot pads from changing from a liquid to a solid phase on the cold ground in winter (Prins 1982a), or perhaps because there are fewer choices for food. Arachidonic acid has a low melting point of -49.5°C, supporting the foot pad theory. Few other plants have arachidonic acid, yet it is present in high concentrations in the blood of Arctic animals, perhaps contributing to increased limb mobility and protecting cell membranes at low temperatures. Interestingly, Hansen and Rossi (1991) found that arachidonic acid comprised 30% of the fatty acids in *Rhytiadelphus squarrosus* (Figure 69) and *Eurhynchium striatum* (Figure 70) at 20°C, but concentrations shifted toward more eicosapentaenoic acid at lower temperatures, with a slight decrease in arachidonic acid.

***Synaptomys borealis* – Northern Bog Lemmings**

The range of the northern bog lemming (*Synaptomys borealis*; Figure 71) extends from Alaska, USA, eastward to Labrador, Canada, and southward to southeastern Manitoba, then southward in the USA to Washington, Montana, and northern New England (Clough & Albright 1987; Cassola 2017).



Figure 69. *Rhytiadelphus squarrosus*, a species in which dominance of arachidonic acid is shifted to dominance of eicosapentaenoic acid at low temperatures. Photo by Johan N., through Creative Commons.



Figure 70. *Eurhynchium striatum* with capsules, a species in which dominance of arachidonic acid is shifted to dominance of eicosapentaenoic acid at low temperatures. Photo by J. C. Schou, with permission.



Figure 71. *Synaptomys borealis*, a species that prefers mossy habitats. Painting by Todd Zalewski, Smithsonian Institutes, through public domain.

Mosses seem to play a prominent role in habitat preference. In the Athabaska-Mackenzie Region of Canada, Preble (1908) reported habitats for the northern bog lemming (*Synaptomys borealis*; Figure 71). These

included the border of a small meadow, a wet, swampy area, proximity of small muskeg ponds, and a marsh. To these, Banfield (1974) reported Canada black spruce bogs as the primary habitat, but also wet subalpine meadows, alpine, and sagebrush. In Churchill, Manitoba, Scott and Hansell (1989) found them in the *Carex*-moss-*Salix* community and the *Salix* community; Wrigley (1974) similarly found them in a sedge-moss tundra (Figure 72). Cowan (1939) found them in muskegs in British Columbia, Canada. Booth (1947) also considered them to be inhabitants of wet, boggy places in the North Cascades, Canada, as did Manville and Young (1965) and Osgood (1904) for Alaska, USA. Groves and Yensen (1989) (also Bursik 1993) reported them from *Sphagnum* bogs (Figure 73) in Idaho, USA, as did Johnson and Cheney (1953) for Idaho and Washington and Laysner and Burke (1973) for Washington. In Montana, Reichel and Beckstrom (1993, 1994) found them in thick mats of *Sphagnum* (Figure 74), and found this habitat to be the best predictor for finding them. For Minnesota, USA, Coffin and Pfanmuller (1988) listed the habitat as dominated by *Sphagnum* and graminoids, including forested bogs and open ericaceous shrublands.

Christian *et al.* (1999) concurred, but expanded the Minnesota habitats to include spruce forest (Figure 73) with moss on the forest floor, wet alpine meadows, and alpine tundra. Clough and Albright (1987) reported them from wet sedge meadows in the northeastern USA. Near the base of Mount Washington, New Hampshire, USA, Preble (1899) found them in swampy habitats densely carpeted with moss. On the other hand, in Montana, USA, Pearson (1991) found them in an old-growth hemlock *Tsuga heterophylla* forest (Figure 75) that lacked the typical bog/fen habitat, although most of the sites were more typical.



Figure 72. Sedge-moss tundra, Nunavut, northern Canada. Photo by A. Dialla, through Creative Commons.

In British Columbia, Canada, Cowan (1939) found that *Synaptomys borealis* (Figure 71) creates a honeycomb of tunnels in the mossy carpets of the muskegs. These tunnels are strewn with fecal pellets, indicating where feeding occurred. The nests are above ground in winter and below ground in summer (Banfield 1974).



Figure 73. Mountain bog/fen in Idaho, USA, with spruce forest in the background. Photo by Robert Marshall, through Creative Commons.



Figure 74. *Sphagnum capillifolium*, a common bog/fen species. Photo by David Holyoak, with permission.



Figure 75. *Tsuga heterophylla* forest. Photo by pxhere, through Creative Commons.

The "house" that is less likely to disappear is a house of *Sphagnum* (Figure 74) (Cowan 1939). The bog lemmings *Synaptomys borealis* (Figure 71) usually live in small colonies among the wet mosses (Osgood 1904). Their runways are among the mosses rather than among the

grasses and other weeds. Although rare even in Alaska, they tend to be more common in peatlands (Preble 1908; Osgood 1909), where they make nests beneath the moss (Headstrom 1970). For these lemmings in their more southern extensions of their range, where they are also rare, it is in the peatlands that they survive (Coffin & Pfannmuller 1988).

Runways not only carry clippings of new bryophyte species, but open habitat to mosses that otherwise could not occur there. Among these in Arctic Alaska is the colonizing species, *Funaria polaris* (Batzli *et al.* 1980).

While it is clear that mosses, especially *Sphagnum* (Figure 74), are important in defining the habitat of the northern bog lemming, it is less clear why. Perhaps a small indication is the presence of *Hylocomiastrum pyrenaicum* (Figure 76) in the mouth of one individual (Harper 1961), but this may just be a gathering to line the nest. Moisture could be an important factor, but there seem to be no physiological studies to test this idea.



Figure 76. *Hylocomiastrum pyrenaicum*, a species that has been seen in the mouth of a northern bog lemming (*Synaptomys borealis*). Photo by Michael Lüth, with permission.

Rand (1945) provides examples that support this suggestion of the importance of moisture. In this study, seven individuals were captured in wet grassy glades and twelve in marshy sedges of dwarf birch flats (Yukon and Northwest Territories, Canada), although another seven trapped by Rand were in typical spruce swamps with mosses. The common factor is moisture.

***Synaptomys cooperi* – Southern Bog Lemming**

The bog lemming (*Synaptomys cooperi*; Figure 77), as its name implies, is a bog species (Connor 1959; Banfield 1974), ranging from southern Manitoba, Canada, south to Arkansas and Tennessee, USA (EOL 2017m). Nevertheless, it can occupy a wide range of habitats, including grasslands, mixed deciduous and coniferous woodlands, spruce-fir forests, and freshwater wetlands (EOL 2017m). In Minnesota, USA, Christian *et al.* (1999) found that it was significantly more abundant in bogs than in sedge meadows or lowland conifer habitats. Connor (1959) reported it from New Jersey. Goodwin (1932) found this species in Connecticut, USA, on a dark forest floor that was overgrown with ferns, *Sphagnum* (Figure 74), and other mosses. No surface runways were visible, but there were definite tunnels beneath the surface.



Figure 77. *Synaptomys cooperi*, bog lemming, makes tunnels under *Sphagnum*. Photo by Phil Myers, through Creative Commons.

Despite its typical bog habitat, Hamilton (1941) found this species in quite different circumstances in Albany County, New York, USA. These "bog" lemmings were in a beech-hemlock forest with a forest floor of spring perennials and lots of black leaf litter. Mosses were apparently not an important component.

The bog lemming eats grasses, sedges, mosses, fungi, fruit, bark, and roots (EOL 2017m). Using fecal analysis, Linzey (1984) found that even in southwestern Virginia, USA, the bog lemming subsisted on the broom grass *Andropogon* (Figure 78) in the summer but on mosses in winter. Both of these foods are low in digestible nutrients.



Figure 78. *Andropogon virginicus*, summer food for the bog lemming (*Synaptomys cooperi*) in Virginia, USA. Photo by P. B. Pelsler, through online permission.

***Dicrostonyx* – Collared Lemming**

Once again, we encounter recent changes in our understanding of the species. *Dicrostonyx torquatus sensu stricto* (Figure 79) is now considered to be distributed only in the Arctic and sub-Arctic tundra and forest-tundra in the Palearctic region – *i.e.*, in Northern Europe and Asia (Wilson & Reeder 2005). *Dicrostonyx* is the only rodent (order **Rodentia**) that changes to white for the winter.

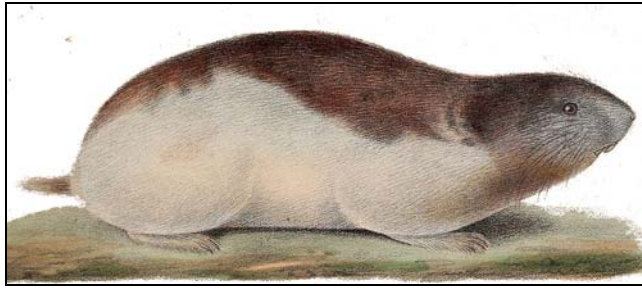


Figure 79. *Dicrostonyx torquatus*, the collared lemming in the Palearctic region. Photo by Ellicrum, through Creative Commons.

Dicrostonyx groenlandicus – Northern Collared Lemming

The northern collared lemming (*Dicrostonyx groenlandicus*; see related species in Figure 80) is distributed in northern Greenland and Queen Elizabeth Islands to northern North America above the tree line, including northern Alaska, USA (Musser & Carleton, in Wilson & Reeder 2005).

Like other genera of lemmings, mosses form part of the diet of *Dicrostonyx*. Not just any moss will do either. It is perhaps not surprising to learn that northern collared lemmings (*Dicrostonyx groenlandicus*) graze on *Polytrichum* (Figure 46-Figure 49) gametophytes during summer on both Devon Island and Ellesmere Island (Pakarinen & Vitt 1974; Longton 1980). But when they were offered fruiting material of *Funaria arctica*, only capsules were eaten (Pakarinen & Vitt 1974). Pakarinen and Vitt suggested that this preference may be related to the high lipid content of some moss spores.

Mosses generally provide less than 10% of the diet of the collared lemming (*cf.* Figure 79) in Alaska (Batzli & Jung 1980). It appears that this Alaskan lemming must now be *Dicrostonyx groenlandicus*, although it was reported as *D. torquatus*. The common sedge *Carex aquatilis* (Figure 81) contains one or more compounds that are deleterious to collared lemmings (Batzli & Jung 1980). The common evergreen shrub (*Ledum palustre*; Figure 82) is likewise deleterious to the collared lemming, but also to the tundra vole (*Microtus oeconomus*; Figure 83) and brown lemmings (*Lemmus sibiricus*; Figure 68). Differing secondary compounds separate the diets of the two lemmings, but the tundra vole is more of a generalist, overlapping the diets of both lemmings.



Figure 80. *Dicrostonyx nelsonii* (= *D. exsol*), one of three North American species, and a bryophyte consumer. Photo courtesy of Tim Menard.



Figure 81. *Carex aquatilis*, a species that is deleterious if eaten by the collared lemming (*Dicrostonyx*). Photo by Matt Lavin, through Creative Commons.



Figure 82. *Ledum palustre* with flowers, a species that is deleterious if eaten by the collared lemming (*Dicrostonyx*). Photo by Kristian Peters, through Creative Commons.



Figure 83. *Microtus oeconomus*, a species that suffers deleterious effects from eating *Ledum palustre*. Photo by анимайна хикари, through Creative Commons.

Gut content analysis indicates that moss capsules form a substantial part of the diet of several North American and Eurasian Arctic lemming species (Batzli & Jung 1980).

And Ron Lewis Smith (Bryonet, 21 November 2006) reports large-scale grazing by lemmings on the capsules of *Polytrichum* (Figure 46-Figure 49) and *Polytrichastrum* (Figure 44-Figure 45) in northern Sweden. When grazing on capsules, lemmings prefer mature capsules in which the spores have a high lipid content (Pakarinen & Vitt 1974).

Wooding (1982) reported the diet of Canadian brown lemmings (*Lemmus trimucronatus*?; Figure 58) was comprised of willow buds, fruits, flowers, grasses, and twigs. However, in captivity they will eat mushrooms and mosses. This supports the concept that availability is an important determinant of the diet. Rodgers and Lewis (1985) came to an interesting conclusion regarding diet differences between the brown lemming (*Lemmus trimucronatus*; Figure 58) and the northern collared lemming (*Dicrostonyx groenlandicus*). The brown lemming preferred graminoids and moss, whereas the northern collared lemming preferred shrubs and herbs. They demonstrated that diet preferences were heritable. The diet preferences for both species were based on macronutrients and caloric content, but the differences between the species depended on secondary compounds and physical characteristics of the plants. They concluded that the northern collared lemming has a greater capacity to deal with secondary compounds or the presence of plant hairs than does the brown lemming.

Myopus schisticolor – Wood Lemming

Wood lemmings, *Myopus schisticolor* (Figure 84), are distributed in the northern Palearctic, ranging from western Norway, through Sweden and Finland through northern and central Russia to the Pacific coast and Sakhalin Island (Russia) (Shenbrot & Krasnov 2005). They live in mossy bogs and coniferous forests in cool climates. In the Ural Mountains, they are rare and are restricted to swampy moss habitats (Bolshakov & Berdjugin 1990). Their runways often traverse moss beds as well as under fallen trees and roots.



Figure 84. *Myopus schisticolor* by its path through the moss *Hylocomium splendens*. Photo by Risto S. Pynnönen, through Wikimedia Commons.

Using food preference experiments, Kalela *et al.* (1963a, b) showed that in northern Sweden, the wood lemmings highly preferred a large number of the most abundant forest mosses, including *Brachythecium*

reflexum (Figure 85), *Dicranum fuscescens* (Figure 86), *D. polysetum* (Figure 10), *D. scoparium* (Figure 11), *Hylocomium splendens* (Figure 63), *Pleurozium schreberi* (Figure 8), *Ptilium crista-castrensis* (Figure 7), *Pohlia nutans* (Figure 55), *Polytrichum commune* (Figure 46), *P. juniperinum* (Figure 48), and *Rhodobryum roseum* (Figure 87). In eastern Finland, *Dicranum* and *Polytrichum* seem to be their favorites, which happen also to have the highest nitrogen content, even though *Pleurozium schreberi* and *Hylocomium splendens* are more abundant (Eskelinen 2002). They rejected most herbaceous species, but only rejected a few bryophytes such as *Ptilidium ciliare* (Figure 9) and *Plagiothecium denticulatum* (Figure 88) (Kalela *et al.* 1963a, b). In one area this species used *Aulacomnium palustre* (Figure 89) extensively, but this seems to be a rare occurrence (Lepp 2008).



Figure 85. *Brachythecium reflexum*, one of the preferred forest mosses of the wood lemming. Photo by Michael Lüth, with permission.



Figure 86. *Dicranum fuscescens*, one of the preferred forest mosses of the wood lemming. Photo by Hermann Schachner, through Creative Commons.



Figure 87. *Rhodobryum roseum*, one of the preferred forest mosses of the wood lemming. Photo by Hermann Schachner, through Creative Commons.



Figure 88. *Plagiothecium denticulatum*, one of the rejected forest mosses of the wood lemming. Photo by Christian Peters, with permission.



Figure 89. *Aulacomnium palustre*, a species that is sometimes eaten as a major food source by the wood lemming. Photo by Kristian Peters, through Creative Commons.

During the snow-free season *Myopus schisticolor* (Figure 84) feeds on only the green topshoots of the mosses, whereas during the snow-covered season, these lemmings bite off the shoots at the base (Kalela *et al.* 1963a, b). Their order of preference in Sweden seems to be

Dicranum scoparium (Figure 11) > *Hylocomium splendens* (Figure 63) > *Pleurozium schreberi* (Figure 64) > *Sphagnum girgensohnii* (Figure 90). This order provides an interesting contrast to the choices of the heather vole (*Phenacomys intermedius*; Figure 18, Figure 21-Figure 22) that Kate Frego described. That vole seemed uninterested in *Dicranum scoparium*. The wood lemming in Finland had some similar preferences to those in Sweden, with *Dicranum* and *Polytrichum* (Figure 46-Figure 49) as top choices, despite a greater availability of *Pleurozium* and *Hylocomium* (Lepp 2008; Figure 91).



Figure 90. *Sphagnum girgensohnii*, a preferred moss for food by *Myopus schisticolor*. Photo by Hermann Schachner, through Creative Commons.

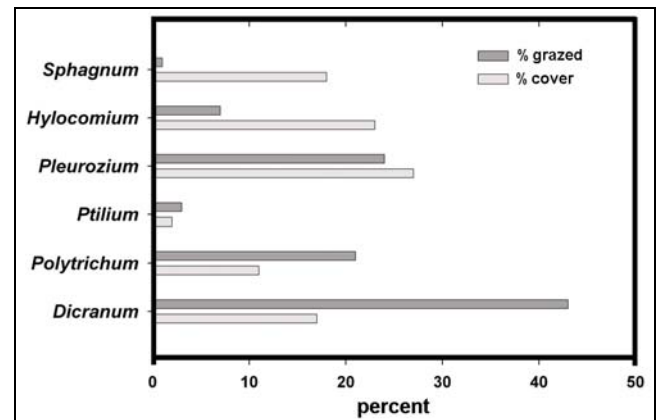


Figure 91. Percent grazing vs cover represented in a lemming habitat in Sweden. Based on data from Lepp 2008.

The species choices changed somewhat in the winter storage holes, which were located in drier sites (Lepp 2008). About 85% of their stored mosses were *Dicranum* (Figure 10), 11% *Pleurozium schreberi* (Figure 64), and only 3% *Hylocomium splendens* (Figure 63). They did still forage in winter, still preferring *Dicranum*, but their second highest nibblings were on *Ptilium* (Figure 7), which occurred in only 30% of the study plots. In fact, for whatever reason, they did not forage on *Polytrichum* (Figure 46-Figure 49) in winter, despite its greater abundance than that of *Ptilium*.

The wood lemming will graze for a long time on the same moss species, hence making it possible to identify its recent food by the color of the feces (Lepp 2008). Those with *Pleurozium schreberi* (Figure 64) and *Hylocomium splendens* (Figure 63) are light brown, *Polytrichum*

(Figure 46-Figure 49) dark brown, *Dicranum* (Figure 10) dark green, and *Ptilium crista-castrensis* (Figure 7) light green.

One explanation for the choice of mosses for the wood lemming may be the nitrogen content (Lepp 2008). *Dicranum* (Figure 10) and *Polytrichum* (Figure 46-Figure 49) have the highest nitrogen content among the mosses in the study area. Secondary compounds such as phenols may discourage consumption of some species that are abundant, but no data are available for the study site. Since such content could differ based on environmental conditions, we can only speculate. On the other hand, Eskelinen (2002) suggested that the high carbon:nitrogen content of *Dicranum* (Caut *et al.* 2009; Codron *et al.* 2011) might account for *Dicranum* as the preferred food, and sometimes only food, for this species in Finland.

Ericson (1977) found that *Myopus schisticolor* (Figure 84) had a high preference for many forest moss species in preference experiments. Their preferred mosses were *Dicranum scoparium* (Figure 11), *Hylocomium splendens* (Figure 63), *Pleurozium schreberi* (Figure 64), and *Sphagnum girgensohnii* (Figure 90). In fact, they rejected most of the herb species. Some bryophytes were also rejected, including the leafy liverwort *Ptilidium ciliare* (Figure 9) and the moss *Plagiothecium denticulatum* (Figure 88). In summer the wood lemming eats only the green tops of shoots, but in winter when the bryophytes are snow covered, they eat them down to the base.

Young wood lemmings cannot survive on mosses alone; to grow faster, they need to eat other plants as well (Andreassen & Bondrup-Nielsen 1991; Lepp 2008). Adults, however, can subsist on mosses alone. Nevertheless, both growth and reproduction are negatively affected when the diet is 100% moss, compared with a diet that also includes grasses and shrubs.

Bathergidae – Blesmoles and Mole Rats

Cryptomys hottentotus – Hottentot Mole-rat

The Hottentot mole-rat (*Cryptomys hottentotus*; Figure 92) is widely distributed in South Africa (Bishop *et al.* 2004). Colonies have 2-14 individuals that permanently live in a network of burrows, locating their food as they burrow (Spinks 1998). The Hottentot mole-rat builds hummocks through its burrowing activity (Lynch 1992) in mesic bog soils (Bishop *et al.* 2004). It may not need a mossy habitat, but some mosses seem to benefit from its presence. The excavated soil is colonized by a lawn-like cover that includes mosses (Lynch 1992).



Figure 92. *Cryptomys hottentotus* (Hottentot mole-rat), a species that creates habitat for some mosses. Photo by Lloyd Glenn Ingles, through Creative Commons.



Figure 93. *Cryptomys hottentotus* adult showing dense fur. Photo by Daderot, through Creative Commons.

Myoxidae – Dormice and Hazel Mice

Muscardinus avellanarius – Hazel Dormouse

In England, the hazel dormouse (*Muscardinus avellanarius*; Figure 94), a somewhat rare nocturnal rodent, gets its name from the Anglo-Norman term *dormeus*, which means "sleepy" (Wikipedia 2008). This refers to its habit of becoming torpid and cold in the winter, waking only occasionally to eat food stored nearby. Hibernation is triggered by temperatures below 16°C (Habrill & Passig 2008).



Figure 94. *Muscardinus avellanarius* – hazel dormouse, a species that uses mosses in its winter hibernacula. Photo by Danielle Schwarz, through Creative Commons.

Its habitat is typically an unshaded understory where there is high species diversity (Bright & Morris 1990). Bright and Morris (1991) contend that this species is entirely arboreal, detouring considerable distances to avoid crossing open ground. They seldom venture more than 100 m from the nest. They seem to prefer nesting in tree hollows, but when these are scarce they select a location with shrub cover and proximity to the forest edge (Berg & Berg 1998). Despite living in trees, they do not seem to include mosses in the diet (Bright & Morris 1993).

Mosses may be more important for a **hibernaculum** (shelter occupied during the winter by a dormant animal). The hazel dormice hibernate in winter, 6-7 months in Lithuania (Juškaitis 1999). Bright and Morris (1996) reported that the dormice covered their surface hibernaculum with a thin layer of mosses or leaves. Such shallow surface hibernacula make the hibernating animals vulnerable to floods, trampling, and predation (Juškaitis 1999).

In a Ukraine study, Zaytseva (2006) found that mosses comprise about 5% of the nesting material in nest boxes used by the hazel dormouse, which sleeps there throughout the day. The globose summer nest is shaped much like a wren's nest with a door (Habril & Passig 2008). Both summer and winter nests often have mosses in them, but the winter nest is more likely to be in a tree hollow or stump. Some dormice may spend their winter on the ground under moss and litter.

Van Laar and Dirkse (2010) examined the nesting materials and found that this species used the epiphytic mosses *Brachythecium rutabulum* (Figure 95) and *Orthotrichum lyellii* (Figure 96). But they also used the primarily ground-dwelling species *Cirriphyllum piliferum* (Figure 97), *Hypnum cupressiforme* (Figure 4), *Calliergonella cuspidata* (Figure 98), *Eurhynchium hians* (Figure 99), and *Thuidium assimile* (Figure 100). All nest materials were pleurocarpous mosses. Van Laar and Dirkse considered the moss choice to be due to the physical properties of the moss that helped the hazel dormouse to maintain a certain degree of humidity in the nests.



Figure 97. *Cirriphyllum piliferum*, a ground species used as nesting material for the hazel dormouse, *Muscardinus avellanarius*. Photo by Michael Lüth, with permission.



Figure 95. *Brachythecium rutabulum*, an epiphyte used for nesting material by the hazel dormouse, *Muscardinus avellanarius*. Photo by Michael Lüth, with permission.



Figure 98. *Calliergonella cuspidata*, a ground species used as nesting material for the hazel dormouse, *Muscardinus avellanarius*. Photo by Tim Waters, through Creative Commons.



Figure 96. *Orthotrichum lyellii*, an epiphyte used for nesting material by the hazel dormouse, *Muscardinus avellanarius*. Photo by Michael Lüth, with permission.



Figure 99. *Eurhynchium hians*, a ground species used as nesting material for the hazel dormouse, *Muscardinus avellanarius*. Photo by Michael Lüth, with permission.



Figure 100. *Thuidium assimile*, a ground species used as nesting material for the hazel dormouse, *Muscardinus avellanarius*. Photo by Hermann Schachner, through Creative Commons.

Gliridae – Dormouse

Glirulus japonicus – Japanese Dormouse

The Japanese dormouse (*Glirulus japonicus*; Figure 101), an endemic to Japan, is nocturnal, searching a relatively large area to find food at night (EOL 2017b). Its name derives from the Anglo-Norman word *dormeus*, which means sleepy one. However, it is not its daytime sleeping that gives it this name, but rather its long hibernation period. The males awaken in May to find a mate.



Figure 101. *Glirulus japonicus*, a species that uses bryophytes in its lair. Photo by Katuuya, through Creative Commons.

It easily climbs trees, where it feeds on seeds, fruits, insects, and bird eggs (EOL 2017b). It can run as easily on the lower side of a branch as on the upper side. This species lacks a caecum, and thus should not be expected to digest cellulose, making mosses an inefficient food and explaining their absence in the dormouse diet.

The Japanese dormouse (*Glirulus japonicus*; Figure 101) uses bryophytes in its lair (Figure 102) (Watanabe

1978), a fact noted much earlier in Britain by Tripp (1888). These bryophytes are useful in building suitable nests. Even in arboreal habitats at warmer latitudes, the Japanese dormouse uses bryophytes for its lair (Watanabe 1978; Minato & Doei 1995; Doei & Minato 1998). After examining 21 nests, Minato and Doei (1995) reported 42 species of mosses and 15 species of liverworts as constituting the majority (53.1% by weight) of the nest materials. Like most of the bird nest bryophytes, the majority of those used by the Japanese dormouse were pleurocarpous, and consistent with the dormouse habitat, they were mostly epiphytic. The six most commonly used species were the leafy liverwort *Frullania tamarisci* subsp. *obscura* (Figure 103), and the mosses *Hypnum tristoviride* (Figure 104), *Isoetecium subdiversiforme* (Figure 105), *Anomodon rugelii* (Figure 106), *Entodon scabridens*, *Anomodon longinervis*. The leafy liverwort *Frullania tamarisci* subsp. *obscura* was often the most abundant bryophyte in the nest. This species is typically abundant nearby, spreading over the surface of tree trunks in large mats, often making it easier for the dormouse to harvest.



Figure 102. *Glirulus japonicus* sleeping in nest. Photo by Yamaneseisokubunpuik, through Creative Commons.



Figure 103. *Frullania tamarisci* subsp. *obscura*, a mat-forming pleurocarpous moss used for nesting material by the Japanese dormouse (*Glirulus japonicus*). Photo from <www.naver.com>, through Creative Commons.



Figure 104. *Hypnum tristo-viride*, a pleurocarpous moss used for nesting material by the Japanese dormouse (*Glirulus japonicus*). Photo by Jiang Zhenyu, Mou Shanjie, Xu Zaiwen, and Chen Jianzhi, through Creative Commons.



Figure 105. *Isothecium subdiversiforme*, a pleurocarpous moss used for nesting material by the Japanese dormouse (*Glirulus japonicus*). Photo from Digital Museum, Hiroshima University, with permission.



Figure 106. *Anomodon rugelii*, a pleurocarpous moss used for nesting material by the Japanese dormouse (*Glirulus japonicus*). Photo by Janice Glime.

Watanabe (1978) found 25 bryophyte species in 8 nests. He found an average of 4 bryophyte species per nest, whereas Minato and Doei (1995) found an average of 6.8 species.

Myoxus glis – Fat Dormouse; Edible Dormouse

The fat dormouse (*Myoxus glis*; Figure 107) occurs throughout much of mainland western Europe and on a number of Mediterranean islands (Milazzo *et al.* 2003).



Figure 107. *Myoxus glis*, a species that eats mosses, but most likely accidentally. Photo by Marcus Ostermann through Creative Commons.

Gigirey and Rey (1998) reported that 12 of 32 stomachs of the fat dormouse, *Myoxus glis* (Figure 107), had moss remains. Gigirey and Rey (1999) subsequently found mosses of this species in the feces. However, in both cases they considered these mosses to be ingested accidentally.

Whereas mosses may not be a desirable diet item, they do provide nesting materials (Drăgoi & Faur 2013). They typically construct these nests using leaves and mosses (Grzimek 2003). The mosses are typically pleurocarpous mosses, including the epiphytes *Brachythecium rutabulum* (Figure 95), *Isothecium myosuroides* (Figure 108), and *Eurhynchium praelongum* (Figure 109), but also nearby forest floor species including *Brachythecium glareosum* (Figure 110), *Ctenidium molluscum* (Figure 111), *Eurhynchium striatum* (Figure 70), and *Eurhynchium hians* (Figure 99) (van Laar & Dirkse 2010).



Figure 108. *Isothecium myosuroides*, a pleurocarpous epiphyte used for nesting by the edible dormouse (*Myoxus glis*). Photo by Malcolm Storey, DiscoverLife, with online permission.



Figure 109. *Eurhynchium praelongum*, a pleurocarpous epiphyte used for nesting by the edible dormouse (*Myoxus glis*). Photo by Janice Glime.



Figure 110. *Brachythecium glareosum*, a pleurocarpous ground species used for nesting by the edible dormouse (*Myoxus glis*). Photo by Michael Lüth, with permission.



Figure 111. *Ctenidium molluscum*, a pleurocarpous ground species used for nesting by the edible dormouse (*Myoxus glis*). Photo by Michael Lüth, with permission.

They locate their nests high in trees, using the cup formed by branching, although some may use abandoned bird nests (Juškaitis 2006).

Dryomys nitedula – Forest Dormouse

The forest dormouse (*Dryomys nitedula*; Figure 112) lives in Switzerland through eastern and southern Europe, Asia Minor and the Caucasus to central Russia and central Asia. It is a tree dweller, living in forests (EOL 2017n).



Figure 112. *Dryomys nitedula*, the forest dormouse. Photo by Domodi, through Creative Commons.

Like *Myoxus glis* (Figure 107), *Dryomys nitedula* (Figure 112) uses mosses in its nests (Drăgoi & Faur 2013). The nests are round with either a side or top entry. The exterior is rough, constructed of branches, but the interior is padded, using grasses, feathers, hair, or mosses. And like the fat dormouse, *Dryomys nitedula* sometimes uses empty bird nests (Adamik & Kral 2008).

Summary

Many rodents have mosses in the gut and feces, but these seem to be the result of accidental intake. But some seem to include them as an important part of the diet, often increasing the percentage in winter. Researchers have suggested that this switch may be a need for nitrogen, arachidonic acid, or fiber. In other cases, it may be a simple matter of availability. The shoot tips seem most desirable for food, but in winter the moss may be clipped at the bottom. Some records indicate that moss capsules are eaten.

Known consumers of mosses include *Chionomys nivalis*, and several members of *Microtus*, *Phenacomys*, *Peromyscus maniculatus* (capsules). Lemmings, in particular, are dependent on mosses in the diet. These may provide arachidonic acid, a more pliable fatty acid at cold temperatures. When their population peaks, they may destroy their moss cover under the snow, making them dangerously visible to predators when the snow melts.

Many rodents use mosses in the construction of nests, particularly as part of the lining. In bogs, several species may coexist in a single bog, some using them for food or to make nests, tunnels, or runways. Pleurocarpous mosses are preferred by most of the rodents that use mosses as nesting materials.

Bryophytes are impacted by the rodents in multiple ways: diminished cover, competition from flowering

plants. But at other times they may benefit. The rodents can serve as dispersal agents, and runways and burrow openings open new habitats where colonizers like *Funaria* can grow, increasing diversity.

Acknowledgments

This chapter has benefitted greatly from anecdotal records sent to me by bryologists and friends who observed these small rodents interacting with mosses in the field. Steve Juntikka, a former plant taxonomy student of mine, sent me an excited email from Isle Royale after observing the young mouse devouring capsules of *Funaria hygrometrica*. Leah Vucetich and Rolf Peterson, Isle Royale researchers, provided me with the identification of the juvenile *Peromyscus maniculatus* based on the picture alone.

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CHAPTER 17-3

RODENTS AND BATS – NON-MUROIDEA

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CHAPTER 17-3

RODENTS AND BATS – NON-MUROIDEA



Figure 1. *Lepus arcticus* in its summer coloring. Photo from Gilad.rom, through Creative Commons.

Soricomorpha

Soricidae – Shrews

In 25 bogs and ombrotrophic mires of Poland, Ciechanowski *et al.* (2012) found that shrews dominated among the mammals captured in pitfall traps. The traps produced 598 individuals distributed among 12 mammal species. Typical wetland species included *Neomys fodiens* (Eurasian water shrew; Figure 2), *Neomys anomalus* (Mediterranean water shrew; Figure 3), and *Microtus oeconomus* (tundra vole; Figure 4). The most numerous species was the Eurasian pigmy shrew (*Sorex minutus*; Figure 5), and it was sometimes the only rodent present in the habitat. It was most common in undisturbed, treeless parts of bogs where *Sphagnum* (Figure 6) dominated.



Figure 2. *Neomys fodiens*, The Eurasian water shrew, a typical wetland species that is found in bogs and mires. Photo from Saxifraga – Rudmer Zwerfer, with online permission.



Figure 3. *Neomys anomalus* (Eurasian water shrew), a typical wetland species that is found in bogs and mires. Photo by Mnolf, through Creative Commons.



Figure 4. *Microtus oeconomus* (tundra vole), a typical wetland species. Photo from Saxifraga, Janus Verkerk, with online permission.



Figure 5. *Sorex minutus* (Eurasian pigmy shrew), the most common rodent species in Polish bogs. Photo from Saxifraga – Rudmer Zwerver, with online permission.



Figure 6. *Sphagnum rubellum*, in a genus that dominates bogs. Photo by Michael Lüth, with permission.

Sorex cinereus – Long-tailed Shrew

The long-tailed shrew (*Sorex cinereus*; Figure 7) occurs from Alaska, USA, east to Labrador/Newfoundland, Canada, south in the USA to Washington, Utah, New Mexico, Northern Great Plains, southern Indiana and Ohio, through the Appalachian Mountains to northern Georgia and western South Carolina, and on the east coast to New Jersey and northern Maryland, where it commonly occurs with mosses (Youngman 1975; Whitaker 2004). It seems often to be present in traps set for lemmings. Hamilton (1941) found *Sorex cinereus* near the summit of Big Black Mountain in Harlan County, Kentucky, USA, at ~1220 m. Of these, six of the seven specimens were taken from runways at the sides of moss-covered logs in damp, deciduous thickets. In the thickets of Maine and New Hampshire, USA, traps set for lemmings also captured shrews (Clough & Albright 1987). These included *Blarina brevicauda* (northern short-tailed shrew; Figure 8) and *Sorex cinereus*. Groves and Yesen (1989) likewise found species of *Sorex* in lemming traps in a *Sphagnum* "bog" in Idaho, USA (Figure 9), as did Pearson (1991) in Glacier National Park and Reichel and Beckstrom (1993) in western Montana.



Figure 7. *Sorex cinereus* (long-tailed shrew), a species that seems to have an affinity for moss-covered logs in its runways. Photo by Phil Myers, through Creative Commons.



Figure 8. *Blarina brevicauda* (northern short-tailed shrew), a species caught in lemming traps in thickets of Maine and New Hampshire, USA. Photo by Gilles Gonthier, through Creative Commons.



Figure 9. Mountain bog (poor fen?) in Idaho, USA. Photo by Robert Marshall, through Creative Commons.

Sciuromorpha

Sciuridae

Records indicating that squirrels use mosses to line their nests are old (Tripp 1888).

Tamias merriami – Merriam Chipmunk

The Merriam chipmunk (*Tamias merriami*) has a small distribution in central and southern California, USA (Harvey & Polite 1999). There seems to be little documentation of chipmunks eating or using mosses. Imagine the surprise when Brent Mishler and his team (Mishler & Hamilton 2002) caught a chipmunk (Figure 10-Figure 11) grabbing a chunk of the moss *Syntrichia princeps* (Figure 12-Figure 13) from the very middle of their field of view (Figure 12) through a CAMcorder (see Grant *et al.* 2006 for setup). Mishler (pers. comm. 12 January 2008) suggests that the Merriam chipmunk (*Tamias merriami*; Figure 10-Figure 11) may have been after the water adhering to the moss (*Syntrichia princeps*), as it had just been moistened earlier in the day for an experiment; the surroundings were dry.



Figure 10. *Tamias merriami*, a chipmunk that harvests mosses. Photo by James Maughn, through Creative Commons.



Figure 11. Chipmunk (*Tamias merriami*), caught in the act by a camcorder as it eats mosses, *Syntrichia princeps*. Photo courtesy of Brent Mishler.



Figure 12. *Syntrichia princeps* with red ellipse indicating where moss was removed by *Tamias merriami*. Photo courtesy of Brent Mishler.



Figure 13. *Syntrichia princeps* with capsules. Photo by F. Guana, Modoc National Forest.

Tamiasciurus hudsonicus – American Red Squirrel

The American red squirrel (*Tamiasciurus hudsonicus*; Figure 14) seems to eat just about anything. It is more tame than most squirrels, and I have even had a confused squirrel climb my leg! It also seems to like decorating its

abode, using paper, moss, and other local objects it can find (Hanrahan 2012).



Figure 14. *Tamiasciurus hudsonicus* (American red squirrel) uses mosses to decorate its home. Photo by Cephas, through Creative Commons b

Sciurus vulgaris – Eurasian Red Squirrel

The Eurasian red squirrel (*Sciurus vulgaris*; Figure 15-Figure 16) is distributed across the northern parts of Europe (Greene 1887). It makes a nest in the fork of a tree. This nest is an interwoven structure of twigs, leaves, and mosses.



Figure 15. *Sciurus vulgaris*, a species that uses pleurocarpous mosses in its nest boxes. Photo from Saxifraga – Mark Zekhuis, with online permission.

Nest boxes used by the Eurasian red squirrel (*Sciurus vulgaris*; Figure 15-Figure 16) displayed pleurocarpous mosses (van Laar & Dirkse 2010). Two of these were ground species [*Hypnum cupressiforme* (Figure 17), *Homalothecium sericeum* (Figure 18)]. The Eurasian red squirrel used only one epiphytic species (*Orthotrichum* sp.; Figure 19), but van Laar and Dirkse suggested that all of the mosses may have been collected from a nearby tree. The nest included ~470 g spruce twigs and ~180 g of these mosses. In addition, the squirrel had included insulation material from the roof of a nearby house. Quinton (1997) reported finding a nest under *Sphagnum* (Figure 6) in the boreal forest of North America.



Figure 16. *Sciurus vulgaris*, a species that uses pleurocarpous mosses as nesting materials. Photo from Saxifraga – Mark Zekhuis, with online permission.



Figure 17. *Hypnum cupressiforme*, a moss used in nests of *Sciurus vulgaris*. Photo by Michael Lüth, with permission.



Figure 18. *Homalothecium sericeum*, a moss used in nests of *Sciurus vulgaris*. Photo by Michael Lüth, with permission.



Figure 19. *Orthotrichum cupulatum* with capsules, a moss used in nests of *Sciurus vulgaris*. Photo by Jutta Kapfer, with permission.

Pullianen and Raatikainen (1996) studied the effect of various nesting materials on nest temperature of the red squirrel in Finland. The wind speed had a large effect on differences between inside and outside the nest. During windless times, the temperature difference could be as much as 30°C in nests made of mosses, proving mosses to be superior insulators to the beard lichen (*Usnea*; Figure 20). Juniper bark provided the poorest insulation among the materials tested. A plastic plate under grass greatly increased the inside temperature by restricting the air current throughout the nest.



Figure 20. *Usnea filipendula*, a nest material that has less insulating ability than the tested mosses. Photo by Jerzy Opiola, through Creative Commons.

TalkTalk (2011) describes the nest of the red squirrel as having a layer of twigs with a layer of moss or bark fragments. It is likely that availability is a major influence on the nest materials used.

***Sciurus carolinensis* – Grey Squirrel**

The grey squirrel (*Sciurus carolinensis*; Figure 21-Figure 22) lives in the eastern USA, but is an invasive in Europe (Steele *et al.* 1996; Goheen & Swihart 2003). It builds a nest the size of a football (YPTE 2011). It is comprised of twigs, often with their leaves remaining attached, and is perched high in a tree. The squirrels line the nest with dry grass, shredded bark, moss, and feathers.

The summer nest is typically flimsy and located among small branches.



Figure 21. *Sciurus carolinensis*, grey squirrel, a species that uses mosses as one of its nest lining materials. Photo by Janice Glime.



Figure 22. *Sciurus carolinensis*, a species that uses mosses as one of its nest lining materials. Photo by John White, with permission.

***Spermophilus parryii* – Arctic Ground Squirrels**

Like the pikas, it appears that Arctic ground squirrels (*Spermophilus parryii*; Figure 23-Figure 24) survive winter in the "warmth" of hibernacula (Barnes 1989). These rodents can wake up and run around when their core temperature is as low as -2.9°C. Temperatures much lower than that can be lethal for such small homeotherms. Maintenance of a temperature as low as -3°C could save up to ten times as much energy as maintenance of a body temperature above 0°C. It is quite possible that for the pikas, the mosses permit the maintenance of sufficiently "warm" temperatures to survive.



Figure 23. *Spermophilus parryii* and tunnel entrances. Photo from National Park Service, through public domain.



Figure 24. *Spermophilus parryii*, Arctic ground squirrel, a species that seems to benefit from the insulating ability of mosses in the nest. Photo Jim McCarthy, through public domain.

Arctic ground squirrels actually cache bryophytes. They preferentially decapsulate bryaceous mosses and store the capsules in their nests for winter food reserves (Zazula *et al.* 2006).

Nest materials for these Arctic ground squirrels in the Yukon include mosses and lichens and these are the most common materials found in the pouches of females (Gillis *et al.* 2005). Carrying these materials was most common prior to and during lactation. These mosses and lichens are absent in male pouches.

***Glaucomys* – Flying Squirrels**

Glaucomys are active all year, but have little resistance to cold (Marchand 2001). Instead, they keep warm by huddling together in tree cavities lined with grass, moss, or bark. The nests can be as much as 30° warmer than the surrounding air outside the nest. These huddles typically have about 10 squirrels, but there may be as many as 50.

***Glaucomys sabrinus* – Northern Flying Squirrel**

The northern flying squirrels (*Glaucomys sabrinus*; Figure 25) has a wide distribution throughout northern North America from Alaska, across Canada to the eastern provinces, with several extensions into northern USA. Like the southern flying squirrel, this squirrel is nocturnal (IUCN 2017).



Figure 25. Northern flying squirrel, *Glaucomys sabrinus*, a species that uses mosses in its nests. Photo by Phil Myers, through Creative Commons.

The northern flying squirrel (*Glaucomys sabrinus*; Figure 25) builds a cavity nest, using various mosses (Patterson *et al.* 2007). Patterson and coworkers found trace amounts of peat moss (*Sphagnum*; Figure 6), dried grasses, cedar leaves, and twigs in the nests in southern Ontario.

***Glaucomys volans* – Southern Flying Squirrel**

The smaller southern flying squirrels (*Glaucomys volans*; Figure 26) occur along the southern USA north to New England (Marchand 2001). They have tiny bodies, weighing only 57-113 g. They are nocturnal, thus most people have never seen them. Nevertheless, they are the most abundant squirrel in the eastern US.



Figure 26. Southern flying squirrel, *Glaucomys volans*, a species that uses mosses in its nests. Photo by Ken Thomas, through Creative Commons.

Lagomorpha – Hares, Rabbits, and Pikas

Leporidae – Rabbits and Hares

***Lepus arcticus* – Arctic Hare**

In the high Arctic, the Arctic hare (*Lepus arcticus*; Figure 1, Figure 27) seems to prefer eating developing bryophyte capsules (Catherine LaFarge, Bryonet 30 March 2016). LaFarge often found decapitated sporophytes, although the lemmings helped in the consumption.



Figure 27. *Lepus arcticus* in white phase. Photo by Chmee2, through Creative Commons.

***Oryctolagus cuniculus* – European Rabbit**

The European rabbit (*Oryctolagus cuniculus*) is present in all Western European countries, Ireland and UK, Austria, Sweden, Poland, Czech Republic, Hungary, Romania, Ukraine, and Mediterranean, Croatia, and Slovakia (Smith & Boyer 2008).

Rabbits, with their noses to the ground, would seem ideally suited for nibbling on bryophytes. However, it seems they may not find them to their liking. Bhadresa (1977) reported that in a food preference test, the rabbit *Oryctolagus cuniculus* (European rabbit – the only domesticated rabbit; Figure 28) in Norfolk – actually disliked *Dicranum scoparium* (Figure 29). But then, that is only one moss. Davidson *et al.* (1990) found leaf fragments of *Mnium* (Figure 30-Figure 31), *Brachythecium* (Figure 32), *Hypnum* (Figure 17), and *Polytrichum* (Figure 36) species in feces of rabbits in southeast England, but never forming more than 5% of the plant material in a fecal pellet. Rabbits eat a mixed diet (European Rabbit 2009), and it appears that mosses may be part of it – or they are ingested accidentally.



Figure 28. European rabbit, *Oryctolagus cuniculus*, a species that consumes at least some mosses. Photo by Aiwok, through Creative Commons.



Figure 29. *Dicranum scoparium* with capsules, a species that the European rabbit dislikes. Photo by Janice Glime.



Figure 30. *Mnium spinosum* cushions, in a genus found in the feces of the European rabbit. Photo by George Shepherd, through Creative Commons.



Figure 31. *Mnium spinosum*, in a genus found in the feces of the European rabbit. Photo by Michael Lüth, with permission.



Figure 32. *Brachythecium rutabulum*, in a genus found in the feces of the European rabbit. Photo by J. C. Schou, with permission.

Rabbits can have a negative impact on bryophytes. After a fire in the heathlands of Brittany, rabbits, along with roe-deer, damaged the bryophytes by scraping (Clément & Touffet 1981). The bryophytes were important as initial colonizers after the fire, so the scraped areas suffered from their loss in succeeding plant and animal colonization. The mosses *Funaria hygrometrica* (Figure 33) and *Ceratodon purpureus* (Figure 34) are important in rebuilding the organic matter following fires and their loss is unfavorable to invertebrate development. *Polytrichum s.l.* species have a strong competitive ability compared to tracheophytes in colonizing these nutrient-poor sites. In particular, *Polytrichastrum formosum* (Figure 35) and *Polytrichum commune* (Figure 36) have a higher density and growth rate and can produce 7-8 tons ha⁻¹ yr⁻¹, preventing new species from becoming established and retarding the growth of those already present. As in cases with other rodents, the rabbits may facilitate the development of these **Polytrichaceae** colonies.



Figure 33. *Funaria hygrometrica*, a species that rebuilds organic matter after a fire. Photo by Michael Lüth, with permission.



Figure 34. *Ceratodon purpureus*, a species that rebuilds organic matter after a fire. Photo by Janice Glime.



Figure 35. *Polytrichastrum formosum* with capsules, a species that is highly competitive on nutrient-poor sites opened up by browsing. Photo from UBC Botany website, with permission.



Figure 36. *Polytrichum commune*, a species that is highly competitive on nutrient-poor sites opened up by browsing. Photo by Michael Lüth, with permission.

But rabbits (*Oryctolagus cuniculus*; Figure 28) can also create habitat for bryophytes. Callaghan (2015) reports that some mosses thrive due to grazing activities by rabbits in the UK. A more spectacular find occurred at an old tin works in Cornwall, where the rare copper moss *Scopelophila cataractae* (Figure 37) benefits by the creation of habitats by rabbits. As succession proceeds on the exposed mineral soil, the tracheophytes replace the bryophytes. However, when the rabbits arrive, the rabbits

create a network of runways and tunnels, exposing the metal-rich soil where the copper moss thrives. These serve as refugia for this moss species that is disappearing as the more coarse vegetation develops. The entrances to burrows are clothed in a mat of protonemata (Figure 38) that have abundant gemmae (Figure 39). Callaghan speculates that the rabbits must disperse thousands of these gemmae on their fur, and the entrance to the tunnel is often the benefactor substrate.



Figure 37. Mature plants of *Scopelophila cataractae*, a species that benefits from rabbits making tunnels. Photo by Blanka Shaw, with permission.



Figure 38. *Scopelophila cataractae* protonemata in a rabbit hole. Photo courtesy of Des Callaghan.



Figure 39. *Scopelophila cataractae* protonema and gemma. Photo by Des Callaghan, with permission.

The European rabbit has multiplied from the 24 introduced to Australia in 1859 to over 600 million in less than a century (European Rabbit 2009), suggesting that this rapid multiplier could present considerable destruction to mosses, or could favor their increase by destroying lichens. In areas where rabbits have been introduced, they often have no natural enemies. Australia is a case in point. In such cases, the virus causing **myxomatosis** may be their only enemy. While this has been used successfully to help control the rabbits, the ones currently remaining in Australia are now immune to it.

In a dune system in Wales, the advent of myxomatosis caused changes in the vegetation. This area had been the site of severe rabbit grazing. In 1954, myxomatosis began to spread to the area and Ranwell (1960) anticipated the loss to the rabbit population. In May of 1955 rabbit pellets were common and thick on the transects across turf areas. Mosses were very evident among the 1-2 cm high turf, but were much less evident in the deep turf. During the succeeding years of rabbit decline, grasses, sedges, and pleurocarpous mosses [*Ditrichum flexicaule* (Figure 40), *Pseudoscleropodium purum* (Figure 41), *Rhytidiadelphus squarrosus* (Figure 42), *R. triquetrus* (Figure 43)] increased, surviving in the ungrazed turf. *Eurhynchium praelongum* (Figure 44) and *Plagiomnium undulatum* (Figure 45) also increased during the study period. At the same time, decreases were evident in the acrocarpous mosses *Bryum* sp. (Figure 46), *Climacium dendroides* (Figure 47), *Dicranum scoparium* (Figure 29), *Syntrichia ruralis* (Figure 48). *Rhodobryum roseum* (Figure 49) disappeared from 1955 to 1958. Overall, the bryophyte richness remained unchanged. The greatest losses of mosses occurred only after 3-4 years of recovery from grazing.



Figure 40. *Ditrichum flexicaule* in Norway, a species that increased when rabbits declined. Photo by Michael Lüth, with permission.



Figure 41. *Pseudoscleropodium purum*, a species that increased when rabbits declined. Photo by Janice Glime.



Figure 44. *Eurhynchium praelongum*, a moss that increased in response to rabbit population decline. Photo by Michael Lüth, with permission.



Figure 42. *Rhytidiadelphus squarrosus*, a species that increased when rabbits declined. Photo by Jan-Peter Frahm, with permission.



Figure 45. *Plagiommium undulatum*, a moss that increased in response to rabbit population decline. Photo by Michael Lüth, with permission.



Figure 43. *Rhytidiadelphus triquetrus*, a species that increased when the rabbit population declined. Photo courtesy of Eric Schneider.



Figure 46. *Bryum caespiticium*, in a moss genus that declined when rabbit population declined. Photo by Bob Klips, with permission.



Figure 47. *Climacium dendroides*, a moss that declined when rabbit populations declined. Photo by Janice Glime.



Figure 48. *Syntrichia ruralis* ssp. *ruralis*, a moss that declined when rabbit populations declined. Photo by Barry Stewart, with permission.



Figure 49. *Rhodobryum roseum*, a species that disappears when rabbit herbivory declines. Photo by Hermann Schachner, through Creative Commons.

The results of Ranwell (1960) differ somewhat from those of Watt (1957), who showed that disappearance of rabbits resulted in the decrease of mosses in ungrazed pasture over long periods of time. Watt found 29 bryophyte species, but *Rhytidiadelphus squarrosus* (Figure 42) is found only in the ungrazed community. This is in contrast to its common presence in grazed pasture on the South Downs and other locations in Breckland, England. On the other hand, 11 species occur exclusively in the

grazed area. These are all small and 10 of the 11 are acrocarpous. As in the Ranwell (1960) study, Watt found that mosses in the ungrazed turf are tall and mostly pleurocarpous. The small mosses seem to be unable to survive competition with taller vegetation, including competition for light. The larger mosses, on the other hand, seem to thrive in the ungrazed conditions. Watt considered these results to support the hypothesis that "in the grazed community the competitive power of the potentially taller growing plants is reduced by grazing sufficiently to allow the smaller species to survive and that in the ungrazed the unchecked growth of taller growing species eliminates or tends to eliminate the smaller, whether they are annual or perennial of varied life-forms."

Gillham (1955) also stressed the importance of rabbit grazing, considering it to be less important than exposure. This contention was supported by the abundance of mosses that are intolerant of extreme exposure, but that are able to reach their maximum in the "closely nibbled swards." Heavy grazing caused moss cover to reach 25%, mostly of the moss *Ceratodon purpureus* (Figure 34) – a moss that is not shy of sunlight. In early spring, when the rabbits were most hungry, the lanes between the grazed heather bushes were dominated by the mosses *Rhytidiadelphus squarrosus* (Figure 42) and *Hypnum cupressiforme* (Figure 17). Gillham (1954) found that bryophyte fragments were only occasionally present in the rabbit dung and concluded that they were probably only eaten when mixed with other plant material. Although the bryophytes are important components of the turf in heavily grazed inland areas, they have little importance on sea cliffs due to their exposure to wind and salt there (Gillham 1955).

Ochotonidae – Pikas

Ochotona princeps – American Pika

The American pika (*Ochotona princeps*; Figure 50) is distributed widely in British Columbia and the western USA (Defenders of Wildlife 2017). Mosses are often a dominant feature of their landscape.



Figure 50. *Ochotona princeps* among mosses. Photo courtesy of Mallory Lambert, through Johanna Varner.

The presence of pikas is usually a good indicator of regions with rocky, mesic, cool habitat (Figure 51) with long winters and short summers (Simpson 2009). Although

the American pikas (*Ochotona princeps*; Figure 51) are a high elevation species in western North America, in the Columbia River Gorge they live near sea level (Horsfall 1925; Varner & Dearing 2014a, b). But at low elevations in the southern part of the Columbia River Gorge, Oregon, USA, the known temperature range was extended and the long winters and typical snow accumulation were not present.



Figure 51. *Ochotona princeps* among the rocks and mosses of a talus slope. Photo courtesy of Johanna Varner.

Dr. Erik Beever (pers. comm.), research ecologist for the National Park Service Inventory & Monitoring program, reported to me that pikas occur at low elevations (less than 150 m) in a valley fed by a snowmelt river in the Cascade Range of western USA. The valley is cold, and he theorizes that their ability to survive the winter without their usual snow cover is due to the thick (>20 cm) moss mats that provide cover and insulation for them (Figure 52).



Figure 52. *Ochotona princeps* emerging from tunnel covered with *Hylocomium splendens* and *Selaginella* sp. Photo courtesy of Johanna Varner.

Varner and Dearing (2014b) supported this assessment, finding that the moss cover insulates the interstices of the talus slopes from temperature fluctuations. Varner and Dearing (2014a) speculated that the mosses could cool the microclimates of the talus in the valley (Figure 51), making the climate suitable for the pikas. The

pikas are able to travel long distances beneath the thick moss cover. Even their extensive moss consumption only removes about 0.002% of the moss in their home ranges in one year. Hence, unlike the lemmings, the pikas can enjoy the cover of the mosses without the danger of eliminating it.

In this unusual habitat they subsist on what is for most rodents an unusual food – mosses (Varner & Dearing 2014a, b). These mosses comprise more than 60% of the diet at the two sites studied. At this rate, the pikas consume ~7.31 g/day and 2.67 kg/year of mosses. The mosses are available all year, thus making food caches unnecessary.

Richardson (1981) considered mosses to be a difficult food for mammalian herbivores, having a high fiber content, low nitrogen, and low digestible energy compared to other food choices. Varner and Dearing (2014a) reported the same high fiber and low nitrogen (<1%) in the mosses of the Columbia River Valley. But the pikas re-ingest their fecal pellets. As a result, the **caecal pellets** (partially digested foods passed as fecal pellets, then re-ingested) of these pikas were far more nutritious, having low fiber content and high nitrogen content, thus allowing the pikas to gain greater nutritional value than that available to other herbivores that do not re-ingest their fecal material.

At high elevations, these talus dwellers forage on the surrounding vegetation (Figure 53) (Huntly *et al.* 1986). Their foraging intensity decreases with distance from the **talus** (rock fragments accumulated at base of cliff or slope), but their selectivity increases with distance, consistent with the "central place foraging theory." In this case, plant abundance increased with distance from the talus. The pikas would travel greater distances to harvest plants for caching (Figure 54) rather than for immediate consumption. For these haying forays, higher proportions of forbs and tall grasses were selected. The haypiles serve to sustain the pikas during winter (Dearing 1997a).



Figure 53. *Ochotona princeps* eating a sedge in the Rockies, a rodent that runs around under the moss layer. Photo by Sevenstar, through public domain.



Figure 54. *Ochotona princeps* (pika) hay pile. Photo courtesy of Bob Krear.

Dearing (1996) tested the hypothesis that plant secondary compounds may be higher in the winter diet either because they function as preservatives or because pikas delay consumption of these species until the toxins degrade. Dearing found little evidence suggesting that morphology excluded any plants from the winter diet, nor was plant size of importance. Even nutrient content showed only a weak relationship. On the other hand, the winter diet was significantly lower in water content and higher in total energy content, but no other nutrients had any consistent pattern. The manipulation of secondary compounds was, however, important. The winter diet contained more total phenolics and had greater astringency.

Dearing (1996) suggested that these secondary compounds helped to preserve the cache, but it also made an additional (initially toxic) food source available. In a follow-up study, Dearing (1997b) found that following 10 months of storage, the winter diet retained 20.5% more biomass with a higher level of energy while being lower in fiber and equal in nitrogen when compared to the summer diet of these pikas. Experiments demonstrated that the pikas preferred foods with a lower phenolic content compared to species with a high content, and they delayed eating those high phenolic species in the haypile until the phenolic content had decreased (due to microbial activity). This need to store a winter cache occupied almost 55% of the surface activity and the evolution of territoriality most likely relates to the need for sufficient vegetation for the winter food cache (Conner 1983).

Behavioral differences between high elevation and low elevation populations of pikas also contributed to their survival at the lower elevations (Smith 1974). At high elevations (3,400 m) the pikas were active throughout the day. At a lower altitude site (2,550 m) they were mostly active in the morning and late afternoon. During their inactive times at high temperatures, survival made it necessary for them to retreat to favorable microclimates among the rockslides. While onset of vocalization and parturition occurred about six weeks earlier at the low altitude site, as one might expect, it seems strange that the onset of hay storage likewise occurred six weeks earlier. But the timing of vocalization and haying were actually correlated with the amount of precipitation during the previous winter. When the winter was dry with little snow and spring was early, the pikas responded by earlier vocalization and haying. [Perhaps the earlier haying was to

ensure more moisture or higher nutrient content of the food items?]

In warm weather, the American pikas have only short bursts of surface activity, typically less than 2.5 minutes at a time (MacArthur & Wang 1974). Instead, they remain in the cooler microclimate beneath the rocks and regulate their body temperature to only 2-3°C below their upper lethal temperature.

The mean body temperature of a pika ranges 37.9-42.7 in an ambient temperature range of -9.3 to 24°C (MacArthur & Wang 1973). Hyperthermia causes death after only two hours of exposure to ambient temperatures higher than 28°C. Its ability to maintain a high body temperature through high metabolism and thick insulation permits it to survive in its high elevation habitat where food storage is limited. Climatic shifts that cause warmer temperatures put the pikas in peril of at least local extinctions (Beever *et al.* 2010). Such local extinctions have already occurred for the American pika living in the Great Basin (Beever *et al.* 2010, 2011). The survival of mosses that ameliorate the high temperatures will be critical to the survival of pikas in these habitats.

Ochotona collaris – Collared Pika

The collared pika (*Ochotona collaris*; Figure 55) is distributed in Alaska and the Yukon (Defenders of Wildlife 2017). They live on a diet of grasses and grass-like plants called sedges, but will include flowering plants, twigs, moss, and lichens among food items. Koju and Chalise (2014) assumed that the poor quality of food in winter caches for this species were due to predation pressure that limited their foraging radius to 10 m.



Figure 55. *Ochotona collaris*, a species that will include some mosses among its food items. Photo by Jacob W. Frank, through public domain.

An interesting mechanism by at least some collared pikas is the selection of food that has previously experienced herbivory by caterpillars (Barrio *et al.* 2013). Could they be seeking food that had higher levels of secondary compounds, stimulated by the herbivore attacks? Or were these herbivore activities signals of suitable food of high quality?

Like *Ochotona princeps* (Figure 50-Figure 54), *O. collaris* (Figure 55) can run across the talus slope under the moss cover (Morrison *et al.* 2004) in its Yukon, Canada, home (Morrison *et al.* 2009). This most likely reduces predation risk as well as modulating the temperatures they

experience (Morrison *et al.* 2004). Nevertheless, choice of food nutrition level does not seem to be dictated by predation risk. On the other hand, in experiments total amount of forage removed by the pikas was inversely related to predation risk.

Erinaceidae – Hedgehogs

The hedgehog (*Erinaceus europaeus*; Figure 56) is the only British mammal to have spines (Wildscreen 2010). They have fairly short tails, long legs, and small ears. When young hedgehogs are born, they have a coat with soft, white spines under the skin to protect the mother during birth. After a few hours these emerge. After about 36 hours, a second coat of dark-colored spines emerges, then later a third set emerges. By day eleven, the hedgehogs are able to curl into a ball, and finally after 14 days their eyes open. They are nocturnal, having large eyes, but they may also be active in the daytime (Wikipedia 2017a). They are solitary animals, and only the female takes care of the young.



Figure 56. The hedgehog, *Erinaceus europaeus*, a species that uses pleurocarpous mosses for nesting materials. Photo by Jörg Hempel, through Creative Commons.

The hedgehog selects pleurocarpous mosses that are available near the nest among its nesting materials (van Laar & Dirkse 2010). The authors suggest that the mosses may be selected to maintain a suitable humidity in the nest.

CHIROPTERA – Bats

Pteropidae – Flying Foxes

Pteropus conspicillatus – Spectacled Flying Fox

The flying fox of Australia is really a kind of bat associated with the rainforest habitats of the Wet Tropics bioregion of northeastern Queensland, Australia (Parsons *et al.* 2007). The spectacled flying fox (*Pteropus conspicillatus*; Figure 57-Figure 58) seems like an unlikely candidate for eating mosses, but... this bat ingests mosses, as evidenced by feces (**splat**) comprised of 14% moss (Andi Cairns, pers. comm. 4 December 2004). Samples from the wet complex notophyll vine forest had the greatest occurrence of bryophytes in fecal samples (22.8% of 685

samples) (Parsons *et al.* 2007). The fragments represented a diversity of bryophytes (15 families of mosses, thallose and leafy liverworts) and ranged from whole plants to detached leaves. The bryophytes evidenced effects of being eaten: highly fragmented, abraded, tightly interwoven with hair and fiber content. The bryophytes mixed with hair suggested that they may have been ingested during grooming.



Figure 57. *Pteropus conspicillatus*, the spectacled flying fox, with folded wings. This bat is a moss disperser. Photo by Shek Graham, through Wikimedia Commons.



Figure 58. *Pteropus conspicillatus* showing the bat wings. Photo by Bernard Dupont, through Creative Commons.

The use of bryophytes as food may be accidental or at least of only minor significance. On the other hand, the flying fox appears to be an effective dispersal vector.

Using material from the interior of the feces (Figure 59-Figure 60), Parsons (Figure 59) and coworkers (2007) demonstrated that 52% of 48 fragments developed rhizoids and/or shoots in culture. Seasonal effects were evident, with those collected early in the season having greater germination success (17 of 28 fragments) than those collected later in the growing season (7 of 20).



Figure 59. *Jennifer Parsons* and splot trap for *Pteropus conspicillatus*. Photo courtesy of Andi Cairns.



Figure 60. *Pteropus conspicillatus* splot on a leaf. Photo courtesy of Andi Cairns.

Summary

Larger rodents make use of bryophytes, particularly for nesting materials, but a few eat them. Bryophytes make habitats for some of these, especially in bogs, fens, and other wetlands, and in Arctic regions. Such common bog dwellers include shrews,

The Merriam chipmunk gathers mosses, presumably for nesting material, but it could possibly be for food. The Eurasian red squirrel uses mosses in its nest, possibly to buffer the temperature, and possibly also explaining use by the Arctic ground squirrels in their hibernacula. Flying squirrels include mosses in the nest, presumably for the same purpose. The grey

squirrel includes mosses to line the nest. The red squirrel uses mosses to decorate its home. Pikas use the mosses as a cool cover during hot days. Pleurocarpous mosses are often preferred for nesting.

Uses for food are less common among these larger rodents, but the Arctic ground squirrels cache moss capsules for winter food. The Arctic hare likewise consumes moss capsules. The European rabbit eats the leafy portions, but it is choosy about which species it eats. Pikas eat mosses when they are abundant. They re-ingest their feces, permitting them to obtain more nutrients from ingested mosses. Even the flying fox (actually a bat) ingests mosses, and in the process it serves as a dispersal agent.

Scraping activity by rabbits can destroy bryophytes, but this favors the growth of *Polytrichum* species and creates disturbed habitats suitable for *Funaria* and *Ceratodon*. And a rabbit burrow provided a suitable habitat (and probably dispersal) for the rare *Scopelophila cataractae*. In Australia, rabbits caused the disappearance of some species and appearance of others, maintaining similar bryophyte species richness. *Rhytidiadelphus squarrosus* benefits from grazing in England, but disappears with rabbit grazing in Australia.

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