CHAPTER 17-1
RODENTS – MUROIDEA: MURIDAE

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CHAPTER 17-1
RODENTS – MUROIDEA: MURIDAE

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.

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.

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?

**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 cristata-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 cristata-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 cristata-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.
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.

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).

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 exclosures 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.
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.

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 enclosure (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
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.

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), and P. denticulatum (Figure 18), Pohlia nutans (Figure 37), and Brachythecium starkei (Figure 38). These small turf or mat species are unable to colonize the wett-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 Di crabrum montanum (Figure 16).
Figure 33. *Microtus* and *Apodemus* tunnels, illustrating destruction of the vegetation. Photo by Marijke Verhagen, Saxifraga, with online permission.

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

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

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

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

Figure 38. *Brachythecium starkei*, a colonizer on rodent runways. 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.

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.

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

**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.

**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. *Drepanocladius 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 enclosure experiments, Austrheim et al. (2007) lumped bryophytes that were difficult to distinguish in the field to avoid taxonomic errors. Those that decreased in the enclosures 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 enclosures.
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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.
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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).

Dispersal

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.](image1)

![Figure 65. *Tetraphis pellucida* gemma, the dispersal unit carried by rodents. Photo by UBC Botany Website, with permission.](image2)

**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 66. *Dicranum flagellare* with brood branches, many of which are broken off and lying on the moss in this image. Photo by Janice Glime.](image3)

![Figure 67. *Micromys minutus*, Eurasian harvest mouse, a mouse that consumes mosses. Photo by Bj. Schoenmakers, through Creative Commons.](image4)
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).

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.

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

The grey red-backed vole (*Myodes rufocanus*; Figure 23) extends through a large range in the northern Palaearctic 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.

![Image](https://via.placeholder.com/150)

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.

![Image](https://via.placeholder.com/150)

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 without any 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).
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 keeni* (mice) in Alaska, the southern red-backed vole preferred habitats with more moss cover than that of *P. keeni* (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.

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

**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).

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**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.](image)

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.](image)

**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).

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. Wetf 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.
Literature Cited


