Glime, J. M. 2018. Rodents – Muroidea: Non-Muridae. Chapt. 17-2. In: Glime, J. M. Bryophyte Ecology. Volume 2. Bryological Interaction. eBook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 19 July 2020 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology2/>.

CHAPTER 17-2
RODENTS – MUROIDEA: NON-MURIDAE

TABLE OF CONTENTS

Cricetidae – Hamsters, Voles, Lemmings, and New World Rats and Mice 17-2-2
  Chionomys nivalis – Snow Vole 17-2-2
  Microtus agrestis – Field Vole 17-2-3
  Microtus pennsylvanicus – Gull Island Vole 17-2-3
  Microtus oeconomus – Tundra Vole 17-2-5
  Microtus pinetorum – Pine Vole 17-2-5
  Microtus xanthognathus – Taiga Vole 17-2-6
  Microtus chrotorrhinus – Rock Vole 17-2-6
  Phenacomys intermedius – Heather Vole 17-2-7
  Phenocomys ungava – Eastern Heather Vole 17-2-7
  Arborimus albipes – White-footed Vole 17-2-8
  Arborimus longicaudus – Red Tree Vole 17-2-8
  Peromyscus maniculatus – Deer Mouse 17-2-9
  Neotoma cinerea – Bushy-tailed Woodrat 17-2-10
  Neotoma fuscipes – Dusky-footed Woodrat 17-2-10
  Neotoma magister – Allegheny Woodrat 17-2-11
  Lemmus – Lemmings 17-2-11
  Lemmus lemmus – Norwegian Lemming 17-2-14
  Lemmus sibiricus/*trimucronatus* – Brown Lemmings 17-2-18
  Synaptomys borealis – Northern Bog Lemming 17-2-20
  Synaptomys cooperi – Southern Bog Lemming 17-2-22
  Dicrostonyx – Collared Lemming 17-2-22
  Dicrostonyx groenlandicus – Northern Collared Lemming 17-2-23
  Myopus schisticolor – Wood Lemming 17-2-24
Bathyergidae – Blesmoles and Mole Rats 17-2-26
  Cryptomys hottentotus – Hottentot Mole-rat 17-2-26
Myoxidae – Dormice and Hazel Mice 17-2-26
  Muscardinus avellanarius – Hazel Dormouse 17-2-26
Gliridae – Dormouse 17-2-28
  Glirulus japonicus – Japanese Dormouse 17-2-28
  Myoxus glis – Fat Dormouse 17-2-29
  Dryomys nitedula – Forest Dormouse 17-2-30
Summary 17-2-30
Acknowledgments 17-2-31
Literature Cited 17-2-31

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 Svíčková, 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 polluters 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 agrestris*** 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.

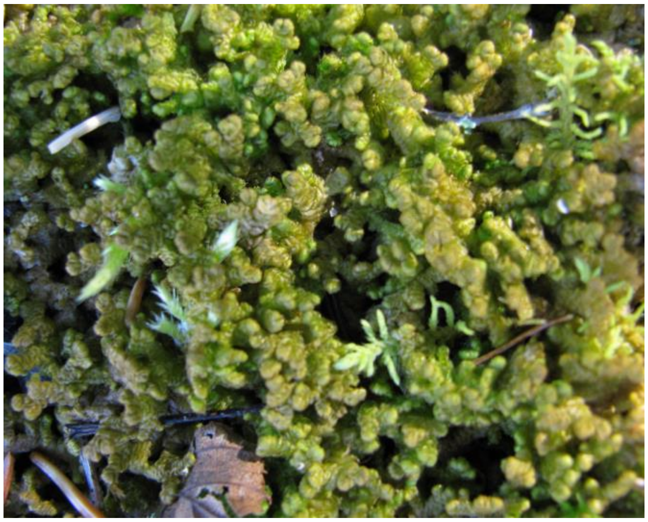

Figure 9. ***Ptilidium ciliare***, a leafy liverwort eaten by ***Phenacomys intermedius***. Photo by Janice Glime.

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 аимаина 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 30ºC (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 lunching 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.

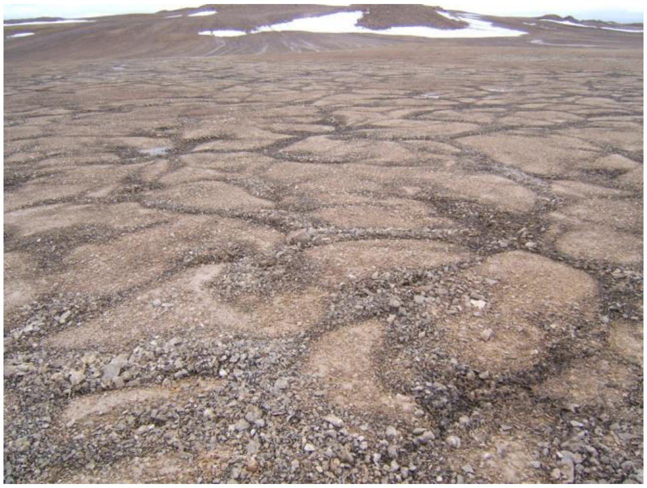

Figure 39. Devon Island showing permafrost. Photo Anthonares, through Creative Commons.

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.

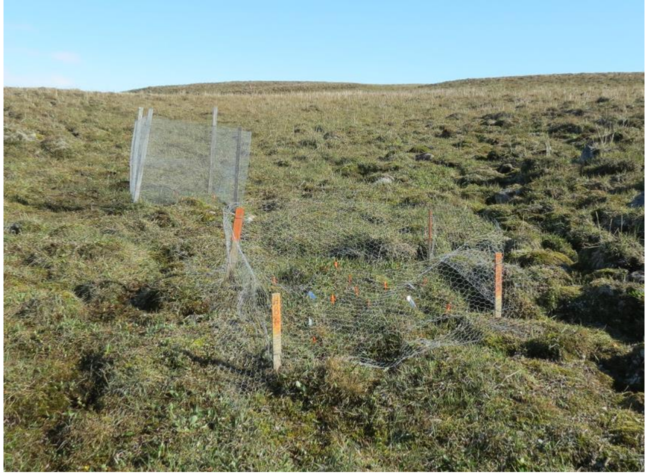

Figure 42. Lemming exclosure 1x1 m on Bylot Island in 2014. Photo courtesy of Dominique Fauteux.

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 Kilpisjaervi 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 exclosure 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 exclosure, 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 exclosures 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), ***Gymnomitrion*** spp. (Figure 52), ***Moerckia blyttii*** (Figure 53)] and the low moss ***Kiaeria starkei*** (Figure 54). ***Kiaeria*** was absent in the exclosures 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 exclosure experiment in a mountain snowbed, the biomass of mosses increased within the exclosures 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 46. ***Polytrichum commune***, a species that can have 3X thicker cover in lemming exclosures. Photo by A. J. Silverside, 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 48. ***Polytrichum juniperinum***, a species that can reach 3X thicker cover in lemming exclosures. Photo by Janice Glime.

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

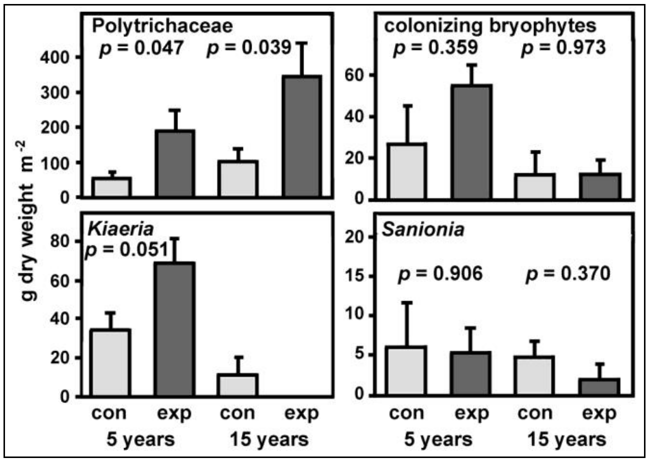

Figure 50. Effect of grazing exclosures (**exp**) compared to controls (**con**) on bryophytes in a lemming habitat at Kilpisjärvi in Finnish Lapland after five and fifteen years of exclosure from herbivory. Redrawn from Virtanen 2000.

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. ***Gymnomitrion 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 exclosure experiments it remained a subordinate species in both exclosures and non-exclosures. 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 exclosures. 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 exclosure 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 exclosures. 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 exclosures. 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 SO_2 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 Palaearctic tundra zone from the White Sea to Kolyma (Russian Federation). Unfortunately, I have found no lemming studies mentioning mosses for the eastern Palaearctic.

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$^{\text{o}}$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 ***Rhytidiadelphus squarrosus*** (Figure 69) and ***Eurhynchium striatum*** (Figure 70) at 20ºC, 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. ***Rhytidiadelphus 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 Layser 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 Pfannmuller (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. Pelser, 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 Palaearctic 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 Palaearctic 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 аимаина 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 Palaearctic, 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.

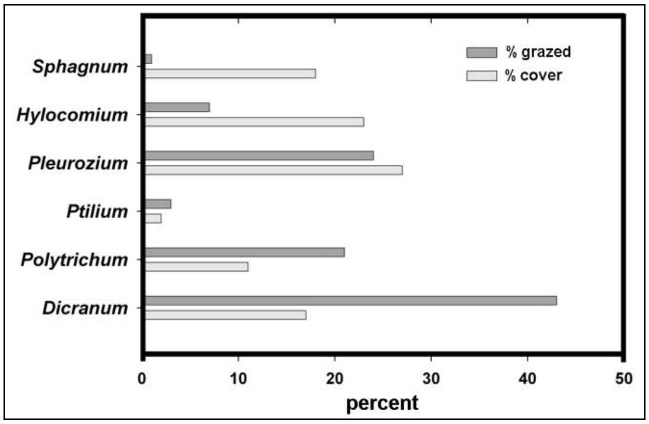

Figure 91. Percent grazing vs cover represented in a lemming habitat in Sweden. Based on data from Lepp 2008.

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.

Bathyergidae – Blesmoles and Mole Rats

Cryptomys hottentotus – Hottentot Mole-rat

The Hottentot mole-rat (***Cryptomys hottentotus***; Figure 92Figure 93) 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 16ºC (Habril & 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 95. ***Brachythecium rutabulum***, an epiphyte used for nesting material by the hazel dormouse, ***Muscardinus avellanarius***. Photo by Michael Lüth, with permission.

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

Figure 97. ***Cirriphyllum piliferum***, a ground species used as nesting material for 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 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 tristo-viride*** (Figure 104), ***Isothecium 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 tamarasci*** 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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