

# CHAPTER 18-1

## LARGE MAMMALS: RUMINANTS - CERVIDAE

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Figure 1. *Rangifer tarandus groenlandicus* scraping and browsing in the Arctic. Photo by Erwin and Peggy Bauer, U.S. Fish and Wildlife, through public domain.

### Ruminantia - Ruminants

Tiny bryophytes seem unlikely foodstuffs for large ruminants, but there are in fact records of their consumption by a variety of these cud-chewing beasts (Figure 2). What seems unlikely is that bryophytes ever provide a major portion of the diet of these animals, and their consumption may often be accidental.

If you have read about "reindeer moss," notably eaten by reindeer and caribou, you have been fooled by an inappropriate common name. The moss in this case is not a moss at all, but a lichen. And a lichen is not even a plant. Rather, it is a fungus with a partner. That partner can be one of the algae (usually Chlorophyta) or one of the Cyanobacteria. Together, they make a whole new type of organism that often can live in places where neither partner can live alone. The fungi provide protection from UV light and from desiccation. The photosynthetic algae or Cyanobacteria provide the carbohydrate energy source through photosynthesis.



Figure 2. Domestic cow (*Bos taurus*) chewing cud. Photo by foxypar4, through Creative Commons.



Wild ungulates may deliberately eat mosses or ingest them accidentally along with a preferred browse. Even large animals such as the Mylakhchinsk bison (Figure 3) have been found with mosses in the alimentary tract (Ukrantseva *et al.* 1978). Peary caribou (*Rangifer tarandus pearyi*; Figure 6) in the Canadian Arctic archipelago can have up to 58% mosses in their rumen (Thomas & Edmonds 1983), hardly indicative of accidental ingestion. Nevertheless, the nutritive value of bryophytes for warm-blooded animals has been questioned (Sugawa 1960).



Figure 3. European bison (*Bison bonasus*); mosses have been found in the alimentary tract of Mylakhchinsk bison. Photo by Michael Gäbler, through Creative Commons.



Figure 4. *Hypnum cupressiforme*; *Hypnum* was found in the alimentary tract of a Mylakhchinsk bison. Photo by Michael Lüth, with permission.



Figure 5. *Polytrichum commune*; *Polytrichum* sp. was found in the alimentary tract of Mylakhchinsk bison. Photo by Rob Routledge, through Creative Commons.



Figure 6. Peary caribou (*Rangifer tarandus pearyi*) in winter. Photo by L. David Mech, through Creative Commons.

High concentrations of polyphenolic lignin-like compounds in cell walls of bryophytes make the cellular contents less accessible to digestive enzymes (Prins 1982). They furthermore often have polyphenols that have antibiotic properties, thus inhibiting the ability of digestive bacteria in ruminants to break down the bryophytes.

Prins (1982) observed that in cold environments mosses are eaten by a variety of herbivores, both mammals and birds, including the ruminants Peary caribou (*Rangifer tarandus pearyi*; Figure 6), Spitsbergen reindeer (*Rangifer tarandus platyrhynchus*; Figure 7), Soay sheep (*Ovis orientalis*; Figure 8-Figure 9), and musk-oxen (*Ovibos moschatus*; Figure 10). Although mosses have similar caloric values to those of tracheophytes, they are difficult for these ruminants to digest (Hegnauer 1962).



Figure 7. *Rangifer tarandus platyrhynchus* grazing among grasses and mosses. Photo by Billy Lindblom, through Creative Commons.



Figure 8. Herd of European mouflon Sheep (*Ovis orientalis musimon*) feeding and lying down, both of which can have an effect on the vegetation. Photo by Frank Vincentz, through Creative Commons.





Figure 9. European mouflon sheep (*Ovis orientalis musimon*), a moss eater. Photo by Frank Vincentz, through Creative Commons.



Figure 10. Musk-ox (*Ovibos moschatus*), a herbivore that eats mosses. Photo through Creative Commons.

One explanation that has been suggested for ruminant herbivory on mosses is that mosses contain high concentrations of highly polyunsaturated fatty acids such as arachidonic acid (Gellerman *et al.* 1972). This fatty acid is also a component of animal cell membranes and other multi-unsaturated C-20 and C-22 fatty acids (Gurr & James 1971; Huneck 1983; Hegnauer 1986). Arachidonic acids have 4 double bonds, whereas the others have 5 double bonds. These are unique in mosses, being absent in seed plants where the highest level of unsaturation is usually two or three double bonds (Swanson *et al.* 1976). Mosses, on the other hand, may have up to 35% of their fatty acids as arachidonic acid, the highest known in any plants (Gellerman *et al.* 1972; Suire & Asakawa 1979). Gellerman *et al.* (1972) and Swanson *et al.* (1976) suggest that in mosses this acid contributes to the special properties of the chloroplast and other tissues that enable them to survive extreme environmental conditions.

Prins (1982) suggested that consumption of mosses with their arachidonic acids permits Arctic animals to have

a higher activity level at low temperatures by making their cell membranes, especially in foot pads, more fluid at low temperatures. These fatty acids decrease the temperature at which the membrane undergoes a phase change from a liquid crystalline state to a solid or gel-like state. This behavior of membranes has been demonstrated for cold-acclimated fish; these fish show a higher degree of unsaturation in the lipids of the cell membrane than do warm-acclimated fish (Caldwell & Vernberg 1970; Cossins *et al.* 1977; Smit 1980). Nevertheless, no direct evidence is available to demonstrate the real fate of arachidonic acid derived from a diet including mosses (Prins 1982). If the Arctic animals do eat mosses to gain arachidonic acid, they may have to eat large quantities because of the limited digestibility of the moss.

Some seeds have been protected from mammal predation by neighboring bryophytes (Ukrainitseva 1979). In the late Pleistocene, bryophytes reduced post-dispersal predation, whereas  $^{14}\text{C}$  dating indicated that some animals had consumed bryophytes.

Van der Wal and Brooker (2004) found that few studies on the impacts of herbivores on the vegetation addressed impacts in the Arctic. They specifically sought understanding of the impact of the moss layer. This layer maintains warmer soils that potentially benefit the tracheophytes. Their results suggest that grazers impact the moss depth, subsequently altering soil temperature, and that this temperature change may impact some tracheophyte abundance. These impacts vary with growth form of the tracheophytes. The moss layer is altered by both grazing and trampling. Furthermore, the feces and urine benefit the tracheophytes, encouraging their expansion.

## Impact of Ruminants on Bryophytes

### Grazing

A number of studies have indicated that heavy grazing reduces bryophyte and lichen dominance in both oceanic and continental areas (Austheim *et al.* 2007). Such reductions favor the establishment or increase of more resistant bryophytes such as *Dicranum* (Figure 11) species and members of the large mosses in the *Polytrichaceae* (Figure 5) (Helle & Aspi 1983; Väre *et al.* 1996; Virtanen 2000; Olofsson *et al.* 2004).

Hanley (1982) considered food selection by ungulates to involve four morphological parameters:

1. body size
2. type of digestive system (caecal or ruminant)
3. rumino-reticular volume to body weight
4. mouth size.

They considered large ungulates and caecal digesters to be limited by time compared to small ungulates and ruminant digesters. The high **rumino-reticular** (part of a cow's four stomachs) volume to body weight ratio adapts them to gaining nourishment from plants such as graminoids with thick cell walls and high cellulose content. Conversely, a low rumino-reticular volume to body weight ratio adapts those animals to thriving on browse plants (leaves, twigs, or other high-growing vegetation) with thin, lignified cell walls.





Figure 11. *Dicranum scoparium*, in a genus favored by heavy grazing. Photo by Michael Becker, through Creative Commons.

Milchunas and Noy-Meir (2002) suggest that such environments as cliffs and other small geological formations that prevent herbivory are likely to have greater diversity. They found that 86% of studies in small refuges indicated positive effects of these refuges on plant diversity, whereas only 50% of large refuges had such an impact.

Takala and coworkers (2012) demonstrated the importance of reestablishing herbivory to restore bryophyte communities that were familiar from the days of pasturing large herbivores in the area. They identified three of these restored bryophyte species as suitable indicators of "valuable" grassland habitats: *Abietinella abietina* (Figure 12), *Climacium dendroides* (Figure 13), *Sytrichia ruralis* (Figure 14). In addition, *Rhytidiadelphus squarrosus* (Figure 15) is indicative of rich soil and survives at least moderate grazing (Ingerpuu *et al.* 1998).



Figure 12. *Abietinella abietina*, a moss indicator of valuable grassland habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 13. *Climacium dendroides*, an indicator of valuable grassland habitat. Photo by Krzysztof Ziarnek, through Creative Commons.



Figure 14. *Sytrichia ruralis*, an indicator of valuable grassland. Photo by David T. Holyoak, with permission.



Figure 15. *Rhytidiadelphus squarrosus* growing among grasses where it seems to benefit from grazing. Photo by Johan N., through Creative Commons.

On the other hand, van der Wal and Brooker (2004) demonstrated that in the High Arctic, mosses can mediate the impact of grazers on the abundance of grasses through their effects on soil temperature.



White-tailed deer (*Odocoileus virginianus*; Figure 16-Figure 17) is among a number of ungulates that have a strong impact on the vegetation in its habitat (Rooney & Waller 2003). Herbivory can cause trophic cascades and even modify the physical structure of the habitat. In the Great Lakes region of North America and elsewhere, the white-tailed deer has experienced population surges due to the annihilation of its natural predators. In response, herb diversity is declining while grasses, sedges, and some ferns are increasing. We can expect that these changes will eventually impact the bryophyte communities (Rooney 2009).



Figure 16. White-tailed deer (*Odocoileus virginianus*) lying down. Photo through Creative Commons.



Figure 17. White-tailed deer (*Odocoileus virginianus goudotii*), a rapidly multiplying species with no natural enemies. Photo by Petrus, through Creative Commons.

Peatlands (Figure 18) seem to be especially susceptible to damage from large herbivores (Bleasdale 1998). The white-tailed deer (*Odocoileus virginianus*; Figure 16-Figure 17), in particular, often enters ombrotrophic bogs and minerotrophic fens in search of food or cover (Pellerin *et al.* 2006). These researchers compared five peatlands (Figure 18) that had been subjected to heavy deer browsing for 75 or more years with five peatlands on deer-free islands. They found that the deer had little impact on cover and species composition in the bogs, but cover of lichens was reduced and that of grasses and sedges increased. But the surface area of bare peat also increased. By contrast, the grazed fens differed significantly from the ungrazed

fens. The floristic composition differed, with plant diversity being greater in undisturbed fens, especially for shrubs, sedges, and liverworts (Figure 29-Figure 31). Dunne and Doyle (1998) documented changes in *Molinia*-dominated (Figure 19) blanket bogs in Ireland, where the impact was caused by Kerry cattle, likewise citing impacts on liverworts.

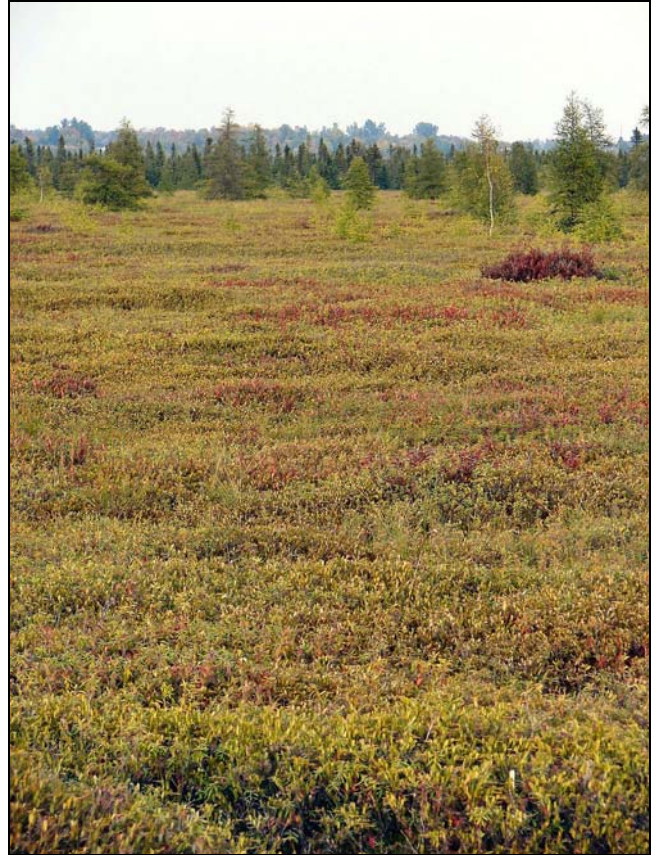


Figure 18. Peatland in Ontario, Canada, a habitat especially vulnerable to browsing and trampling. Photo through Creative Commons.



Figure 19. *Molinia* (= *Melica*) *caerulea* in wetland, a blanket bog species where cattle can change the bryophyte vegetation. Photo by Lamiot, through Creative Commons.

The effects are not the same in all ecosystems. Olofsson *et al.* (2002) used exclosures against herbivores in two Arctic-alpine (Figure 20) plant communities. Exclosures in the snowbed (Figure 21-Figure 22) resulted



in significant biomass increases of both tracheophytes and cryptogams (including bryophytes), but no corresponding changes occurred in the tall herb meadow. The least competition occurred in the open snowbed plots, a condition the researchers attributed to the mammalian herbivores. Excluding the herbivores permits the plant biomass to build up and eliminate the competitive differences.



Figure 20. Arctic landscape. Photo from USFWS, through Creative Commons.

In northwestern Finnish Lapland, Pajunen *et al.* (2008) used exclosures from 1999-2006 to compare the effects of reindeer grazing in a forest-tundra ecotonal area (Figure 21). The area included tundra heath, frost heath, and riparian habitats. They found a general increase in total cover in all exclosures. However, while the dominant tracheophyte groups increased, the bryophytes diminished in both cover and species richness within the exclosures. Like the cattle, it appears that the reindeer maintain a habitat suitable for bryophytes by reducing tracheophyte competition for light.



Figure 21. Forest-tundra ecotones in Rocky Mountain National Park, USA. Photo by Michael Kirsh, through Creative Commons.

Van der Wal and Brooker (2004) investigated the impact of large herbivores on Arctic plant communities (Figure 22-Figure 23), particularly with attention to the impact on the depth of the moss layer. They found that grazing had a domino effect by impacting the depth of the moss layer (Figure 22-Figure 23), subsequently causing a rise in the soil temperature (see Figure 25 for moss effect on soil temperature). That, in turn affected the seed plant abundance and community structure, especially promoting

growth of grasses. The grazing and trampling are both effective in reducing the depth of the moss layer. The grasses benefit not only from the warmer temperatures, but also from the added nutrients from grazer feces (poop) and urine.



Figure 22. Moss layer at Nunavut tundra, Northern Canada, showing late snowbed. Photo by A. Dialla, through Creative Commons.



Figure 23. Vegetation in the tundra at Nunavut in the Canadian Arctic Archipelago. Photo by A. Dialla, through Creative Commons.

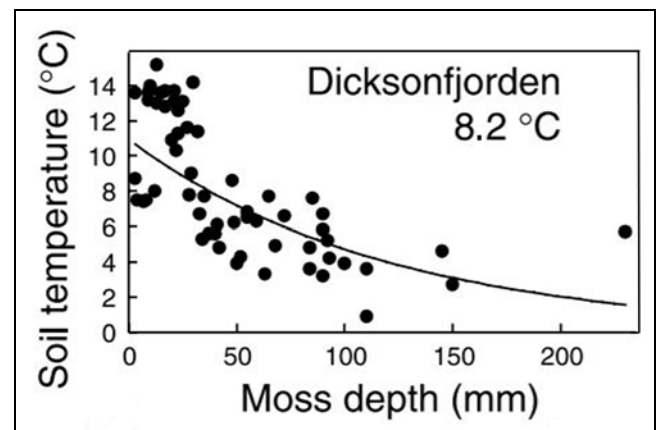


Figure 24. Typical example of moss depth effects on soil temperature in Spitzbergen. Temperature given is ambient temperature at Dicksonfjorden. Modified from van der Wal and Brooker 2004.



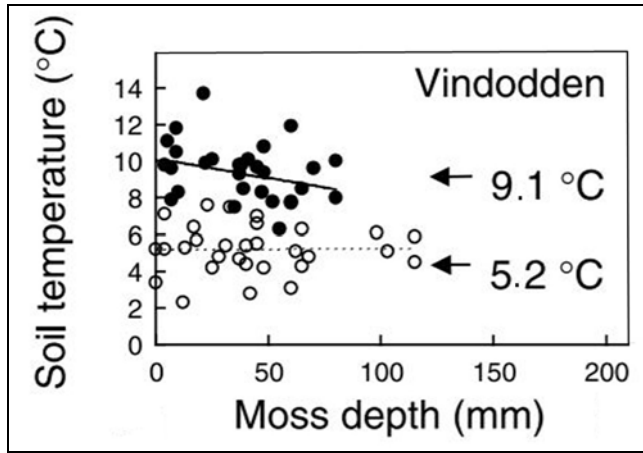


Figure 25. Typical example of moss depth effects on soil temperature at Vindodden in Spitzbergen. Dark and open circles represent two different days with different ambient air temperatures, as indicated. Modified from van der Wal and Brooker 2004.

Similarly, Elkington (1981) found that sheep and rabbit enclosures on limestone grasslands (Figure 26) in Teesdale, England, caused the grassland structure to become more open, largely through the loss of the grass *Festuca ovina* (Figure 27) and reduction of bryophyte and lichen cover. In Utah, USA, the cryptogamic crust (Figure 28) suffered "considerably" from domestic grazing (Anderson *et al.* 1982a, b). In this sensitive ecosystem, the cryptogamic cover was able to recover in 14-18 years.



Figure 26. Limestone grassland in Swindale Wood, England. Photo by Andrew Curtis, through Creative commons.

Porley and Rose (2001), being bryologists, expressed regret that the liverwort mat (*Scapanietum asperae*; Figure 29-Figure 39) was disappearing in English chalklands, dropping from 30 known localities 50 years earlier to 8 or fewer. These communities consisted of the bryophytes *Scapania aspera* (Figure 29), *Frullania tamarisci* (Figure 30), *Porella arboris-vitae* (Figure 31), *Hypnum lacunosum* (Figure 32), *Ctenidium molluscum* (Figure 33), *Dicranum scoparium* (Figure 11), *Pseudoscleropodium purum* (Figure 34), *Calliergonella cuspidata* (Figure 35), *Neckera crispa* (Figure 36), *Homalothecium lutescens* (Figure 37), and occasionally *Ditrichum gracile* (Figure 38) and *Tortella tortuosa*

(Figure 39). These communities have suffered from release from grazing, being replaced by other species. The loss for bryologists is supported by the absence of these communities on the continental chalklands and the conservation importance of the community.



Figure 27. *Festuca ovina* var. *glauca*, a grass lost to grazing in limestone grasslands. Photo by David J. Stang, through Creative Commons.



Figure 28. Cryptogamic crust in Hovenweep National Monument (in Colorado and Utah). Photo from NOS, through Creative Commons.



Figure 29. Leafy liverwort, *Scapania aspera*, dominant species in the liverwort mat (*Scapanietum asperae*). Photo by Hermann Schachner, through Creative Commons.





Figure 30. *Frullania tamarisci*, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo from Proyecto Musgo, through Creative Commons.



Figure 31. *Porella arboris-vitae*, a leafy liverwort member of the liverwort mat in English chalk grasslands. Photo by J. C. Schou, with permission.



Figure 32. *Hypnum lacunosum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 33. *Ctenidium molluscum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 34. *Pseudoscleropodium purum*, a moss member of the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 35. *Calliergonella cuspidata*, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.





Figure 36. *Neckera crista*, a moss member of the liverwort mat in English chalk grasslands. Photo by Uniprot, through Creative Commons.



Figure 37. *Homalothecium lutescens*, a moss member of the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.



Figure 38. *Ditrichum gracile*, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by Hermann Schachner, through Creative Commons.



Figure 39. *Tortella tortuosa*, a moss that sometimes occurs in the liverwort mat in English chalk grasslands. Photo by David T. Holyoak, with permission.

As late as 1997, Bullock and Pakeman voiced concerns over the effects of reintroducing grazing to lowland heath (Figure 40) in England, citing the lack of information to guide management in these ecosystems. They found that introducing grazing or increasing stocking rates caused a general increase in plant species richness, grass, forb, bryophyte, and lichen cover, and area of bare ground. At the same time, litter depth and cover of dwarf shrubs and scrubs.



Figure 40. Lowland heath in England, a habitat that suffers from the effects of over-grazing. Photo by Roger Key, with permission.

One source of understanding the impact of browsers is through introductions. The Sitka black-tailed deer (*Odocoileus hemionus sitkensis*; Figure 41-Figure 42) to Haida Gwaii in the Queen Charlotte Islands, BC, Canada, in the late 19th Century provided such an opportunity (Stockton *et al.* 2005). The temperate rainforest is a habitat where little information exists on the impact of herbivory by large mammals. This system fortunately gave us a time table because among the 7 islands, there was representation of no deer, deer for less than 20 years, and deer for more than 50 years. When the deer were introduced, their natural predators (wolves and cougars) were absent. Where deer were never present, lower vegetation cover exceeded 80%, whereas it was less than 10% on islands that had



experienced deer browsing for more than 50 years. Interestingly, species richness was similar on all 7 islands, whereas diversity at the plot scale (314 m<sup>2</sup>) was 20-50% lower on islands with more than 50 years of deer browsing. Hence, the deer have simplified the ecosystem. This raises the question of the effects on bryophytes in this temperate rain forest. Typically, bryophyte cover is high, and the forests on Queen Charlotte Island are draped in bryophytes (Figure 43) (e.g. Hong & Glime 1997).



Figure 41. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), a species that has devastating effects on vegetation on some islands among the Queen Charlotte Islands, British Columbia, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 42. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). Photo by Wanetta Ayers, through public domain.



Figure 43. Hoh rainforest, with epiphytes on maples, a scene similar to that on the nearby Queen Charlotte Islands. Photo by Kevin Muckenthaler, through Creative Commons.

Contrary to many of these studies, Suominen *et al.* (1999) demonstrated in two Swedish pine forests (Figure 44) that moss cover was higher in unbrowsed plots (by moose, *Alces alces*; Figure 45), and lichen cover was higher in browsed plots. They considered this difference to be a response to the differences in the amount of light reaching the forest floor. In the greater light, the drought-resistant lichens could outcompete the shade-tolerant mosses, reaffirming the differences in response between habitats. Invertebrates differed as well, with higher numbers in unbrowsed plots, but diversity was higher in the browsed plots. This is an aspect that has not been examined relative to bryophyte communities of invertebrates. It also raises the question of the impact of moose browsing on the epiphytic bryophyte flora. Even if the mosses are not eaten, the higher light and lower moisture levels caused by browsing on trees could have an impact.



Figure 44. Pine forest in Sweden. Photo from Pixabay, through Creative Commons.



Figure 45. *Alces alces* bull moose grazing among shrubs. Photo from Denali National Park, Alaska, USA, through Creative Commons.

Brotherson *et al.* (1983) examined the long-term effects of grazing on **cryptogamic crusts** (bryophytes, lichens, algae, and bacteria; Figure 28) in the Navajo National Monument, Arizona, USA. They found that grazing over 40 years had greatly impacted both the



**tracheophyte** (plants with lignified vascular tissue) and cryptogamic communities. The cryptogamic community suffered the most, exhibiting the greatest reduction in cover. Algae were much more tolerant than the lichens and bryophytes. In Idaho, Hilty *et al.* (2004) suggested that following fire in these rangelands, a resting period from livestock grazing would reduce invasive grasses and benefit the native mosses.

Not surprisingly, air pollution, in particular nitrogen pollution, plays a role in the relationship of grazing and bryophytes. Van der Wal *et al.* (2003) found that as livestock grazing increased concurrently with increased N deposition, large-scale degradation of both natural and seminatural ecosystems occurred. Using an experimental approach, these researchers demonstrated that the interplay between grazing and N deposition has led to the replacement of moss-dominated habitats by those dominated by grasses and sedges.

### Trampling

Even when large mammals don't eat bryophytes, they can impose serious damage through trampling (Figure 46). Liddle (1997) considered mosses to be particularly sensitive to disturbances such as trampling. Thus, when trampling is reduced, we should expect bryophyte abundance to increase (Jónsdóttir 1991; Økland 1997; van der Wal *et al.* 2003). But the response is not quite so simple, because it also depends on the response of the rodent community (Austrheim *et al.* 2007). This trampling effect becomes most important in sensitive, slow-growth ecosystems such as those in the Arctic (Callaghan *et al.* 2001).



Figure 46. Introduced reindeer on South Georgia, Ocean Harbour, showing how hoofs could kick up and trample the vegetation. Photo by Roger S. Key, with permission.

In addition to trampling, some hoofed mammals such as roe deer (*Capreolus capreolus*; Figure 47) scrape the ground (Figure 48), dislodging the bryophytes and often exposing bare ground (Clément & Touffet 1981).

Although the role in destruction creates a major impact, trampling and scraping (Figure 1) can at times facilitate dispersal of bryophytes. Péntes-Kónya (2003) documented the role of disturbance in dispersal of the cushion moss, *Leucobryum juniperoides* (Figure 49), in the Bukk Mountains of northern Hungary where it is the

dominant bryophyte on the ground. Both deer (*Cervidae*) and mouflons (*Ovis orientalis orientalis*, a subspecies of wild sheep) are instrumental in turning over whole cushions during the extremely dry spring. But *L. juniperoides* actually benefits somewhat from this behavior. It responds to the change in light direction and gravitational pull by growing in a ball (Figure 50). And it has **caducous** (able to break off) leaves that behave like gemmae for reproduction (Figure 51).



Figure 47. Roe deer (*Capreolus capreolus*) male and female. Photo by Juan Lacruz, through Creative Commons.



Figure 48. Roe deer (*Capreolus capreolus*) tracks, indicating the depth of penetration of hoofs. These same hoofs can carry bryophyte fragments and "plant" them elsewhere. Photo by James K. Lindsey, with permission.



Figure 49. *Leucobryum juniperoides*, a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by David T. Holyoak, with permission.





Figure 50. *Leucobryum juniperoideum* cushion that has been turned upside down and experienced new growth on its new top side. This ball-shaped form is typical after such disturbance. Photo courtesy of Erika Péntzes-Kónya.



Figure 51. Leaf of *Leucobryum juniperoideum* that was turned to under side of clump, showing the development of rhizoids. Photo courtesy of Erika Péntzes-Kónya.

While the stems of *L. juniperoideum* are upside down, rhizoids form on the leaf tips (Figure 51). These plants, and their detached tips, form new plants and can be dispersed by the hooves. Even the leaf lamina cells can produce filaments when the plants are turned over (Figure 52). Nevertheless, during the dry season the disturbance is greater than the regeneration. The new growth occurs faster in the rainy periods. *Leucobryum glaucum* (Figure 53-Figure 54) has similar behavior when turned upside-down (Erika Péntzes-Kónya, Bryonet 13 June 2011).

But cryptogamic crusts (Figure 28) are not so fortunate (Anderson *et al.* 1982b). Domestic grazing greatly reduces the lichens, mosses, and algae forming the crusts. This destruction coincides with soils with heavier texture and greater salinity. Recovery seems to be moderately fast, with crusts usually becoming re-established within 14-18 years.

In three sagebrush communities (Figure 55) in east-central Idaho, USA, cryptogamic crusts (Figure 28; Figure 55) are important in maintaining the ecosystem (Kaltenecker *et al.* 1999). These biological crusts typically

have bryophytes that help to retain water and collect it from dew. Following ~10 years of enclosure to browsing, the crust doubled compared to areas where browsing continued. However, in the area of low sagebrush (*Artemisia arbuscula*; Figure 56), there was the least crust cover and this cover did not differ in exclusion areas there, apparently limited by the gravelly soil surface and dominance of rhizomatous grasses.

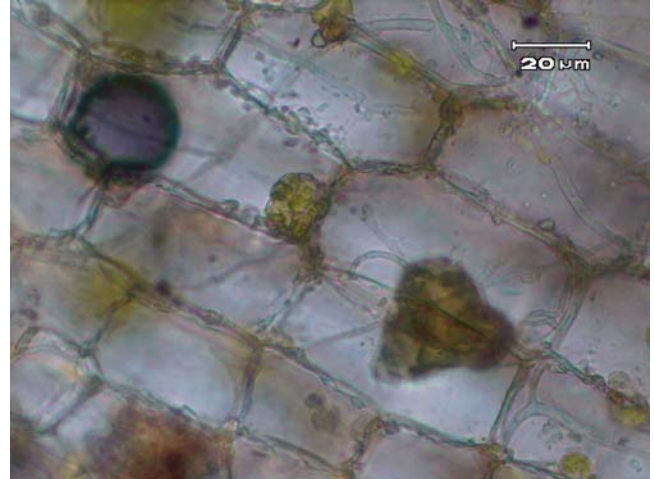


Figure 52. Green cells of *Leucobryum juniperoideum* that developed filaments when moved to the top of the clump. Photo courtesy of Erika Péntzes-Kónya.



Figure 53. *Leucobryum glaucum* in Epping Forest. Photo by Barry Samuels, with permission.



Figure 54. Cushion moss (*Leucobryum glaucum*), a species that forms a ball and grows on the new upper side when turned over by disturbance. Photo by Rob Routledge, through Creative Commons.





Figure 55. Sagebrush steppe in Grand Teton National Park, USA. Photo by Matt Lavin, through Creative Commons.



Figure 56. *Artemisia arbuscula*, a sagebrush in areas where cryptogamic crusts are limited. Photo by Matt Lavin, through Creative Commons.

Yet another response to trampling can be found in fens (Figure 57) (Stammel & Kiehl 2004). Low light availability limits seed germination, accompanied by litter accumulation and competition by mosses.



Figure 57. Fen, sometimes referred to as a flow-through bog. Photo through Creative Commons.

## Manuring

We use manure (Figure 58) to fertilize crops, so it is reasonable to ask what effect ruminant manure has on the one-cell-thick moss leaves. Vanderpuye *et al.* (2002) examined the effects in the *Luzulion nivalis* (Figure 59) snowbeds (Figure 60 at Sassendalen, Svalbard). This location has a low water table, whereas moss tundras usually have no standing water. In these cold environments, manure seems to explain the moss tundra vegetation. The mammals contributing this manure are non-migratory Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7).



Figure 58. Manure-straw mix to be used in agriculture. Photo by Malene Thyssen, through Creative Commons.



Figure 59. *Luzula nivalis*, the species for which the *Luzulion nivalis* is named. Photo by Jeffery M. Saarela, through Creative Commons.





Figure 60. Late snowbeds, Great Britain. Photo by Nigel Brown, through Creative Commons.

Several authors have demonstrated that manure from mammalian grazers and enhanced nutrient cycling resulting from grazing can cause an increase in the graminoids and a concurrent decrease in bryophyte abundance in Arctic-alpine tundra (Olofsson *et al.* 2001; Stark *et al.* 2002).

Van der Wal *et al.* (2004) tested the hypothesis that large herbivores manipulate their own food supply by modifying soil nutrient availability. To do this in a Spitzbergen tundra, they added feces of the reindeer *Rangifer tarandus platyrhynchus* (Figure 7) for four years, thus simulating the effect of feces impact by a larger herd. After the third year, the standing crop of grasses had clearly increased in both shoot density and biomass per shoot. At the same time, the increase in feces and grass productivity did not result in increased grazing pressure. The added feces caused an increase in soil microbial biomass carbon and nitrogen, especially under wet conditions that promoted decay rates. Under dry conditions, the grasses benefitted from the fecal additions. On the other hand, the moss layer depth was significantly impacted by the fecal addition. Areas with the greatest soil microbial biomass likewise had the greatest reduction in moss depth. Van der Wal and coworkers suggested that the moss reduction was due to greater decomposition of the mosses by the enhanced microbes. It is common for Arctic seabirds to affect the tundra vegetation, but here the non-migratory Svalbard reindeer have replaced the seabirds and created an intense manuring effect (Vanderpuye *et al.* 2002). This illustrates yet another mechanism by which grazers impact the bryophyte community, especially in the tundra (van der Wal *et al.* 2004). But Vanderpuye and coworkers consider the reindeer manuring to explain the presence of moss tundras in this Spitzbergen landscape where seabird colonies are absent. Perhaps it is all about the size of the herd.

### Life on Manure – Splachnaceae

A discussion of manuring and bryophytes would not be complete without describing the fascinating relationships of the moss family **Splachnaceae** with manure.

While some bryophytes suffer from the manure of reindeer and caribou, others find these to be their most suitable habitat. These dung mosses include, in particular, many members of the **Splachnaceae**. Included are *Aplodon wormskjoldii* (Figure 61), *Splachnum luteum* (Figure 62), *S. sphaericum* (Figure 63), *Tayloria* spp. (Figure 64), *Tetraplodon mnioides* (Figure 65), *T. paradoxus* (Figure 66), and *Voitia hyperborea* (Figure 67) (Steere 1976). See also Volume 1, Chapter 4-9, Adaptive Strategies: Spore Dispersal Vectors.



Figure 61. *Aplodon wormskjoldii* with capsules, an Arctic dung moss. Photo by Taimyr Anabar Fedosov, with online permission.



Figure 62. *Splachnum luteum* in Alaska, a dung moss with its capsules. Photo courtesy of Andres Felipe Baron Lopez.



Figure 63. *Splachnum sphaericum* with capsules, an Arctic dung moss. Photo by Madcowcult, through Creative Commons.





Figure 64. *Tayloria serrata* with capsules, an Arctic dung moss. Photo by Hermann Schachner, through Creative Commons.



Figure 65. *Tetraplodon mnioides* with capsules, a dung moss in the Arctic. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *Tetraplodon paradoxus* with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.



Figure 67. *Voitia hyperborea* with capsules, a dung moss in the Arctic. Photo by Michael Lüth, with permission.

I am most familiar with these mosses on moose droppings. My first experience was spectacular. I was walking along a path on Isle Royale (Figure 68-Figure 69), Michigan, USA. This is the largest island in Lake Superior (Figure 68) and has a large moose (*Alces alces*) population. My student was ahead of me, searching for the *Splachnum rubrum* (Figure 70-Figure 71) he had seen before I arrived. Suddenly an iridescent purplish red caught my eye! My immediate response was "What in the world?...IT'S SPLACHNUM!"



Figure 68. Lake Superior, with Isle Royale indicated by the arrow. Photo from NASA, through public domain.



Figure 69. Isle Royale and its associated smaller islands. Photo by Todd VerBeek, through Creative Commons.





Figure 70. Winter moose dung with *Splachnum rubrum* on Isle Royale. Photo by Janice Glime.



Figure 71. *Splachnum rubrum* capsules on Isle Royale, Michigan. Photo by Janice Glime.

*Splachnum rubrum* (Figure 70-Figure 71) is picky, occupying only the winter dung (Figure 72), the dung that drops as small cylinders. It differs from the large, moist "cow pies" of summer because the winter food consists of twigs and branches and other foods low in nutrients and moisture content.



Figure 72. Moose (*Alces alces*) winter scat. Photo by Cephas, through Creative Commons.

In spring, the capsule odor attracts flies. With luck, the flies have visited another patch of these dung cylinders where *Splachnum rubrum* (Figure 70-Figure 71) has grown and produced capsules. In their mature stage, these capsules smell like dung and attract the flies that subsequently get spores on them. These are transferred to the next patch of dung they encounter. Details of this wonderful family will be provided later in the Habitats volume.

## Cervidae – Deer, Elk, Moose, and Caribou

In the Arctic, members of this family are often dependent on mosses for food, but some members of the family may also impact bryophytes in lower latitudes. Chollet *et al.* (2013) reported that the deer family **Cervidae** has increased in abundance in temperate and boreal forests. The impact of these over-abundant deer is well documented (Kirby 2001), but little is known about the impact on bryophytes (Chollet *et al.* 2013).

### White-tailed Deer – *Odocoileus virginianus*

The white-tailed deer (*Odocoileus virginianus*; Figure 73) has a significant impact on the tracheophyte vegetation, damaging forest vegetation and crops (Horsley *et al.* 2003). Using exclosures (Figure 74), Stewart and Burrows (1989) found that the lichen-moss cover changed little between exclosures and non-exclosures from 1979 to 1985.



Figure 73. *Odocoileus virginianus*, white-tailed deer, seems to have little effect on the bryophyte vegetation. Photo by Scott Bauer, USDA, through public domain.



Figure 74. Exclosures, near for reindeer, far (with young trees) for both rodents and reindeer, at Abisko in sub-Arctic Sweden. Photo by Monteux, through Creative Commons.



In many parts of the eastern USA the increases in deer populations indicate that effects on plant communities may increase in the future (Stromayer & Warren 1997). The impact of heavy deer browsing seems to be particularly exacerbated in swamps by the mossy and soupy peat. Quantitative studies are needed to assess the impact of the white-tailed deer on bryophyte communities.

### Black-tailed Deer – *Odocoileus hemionus*

Chollet *et al.* (2013) compared the impact of browsing by the black-tailed deer (*Odocoileus hemionus*; Figure 75-Figure 76) in two island groups, one with the deer and one without, in the Haida Gwaii archipelago of British Columbia, Canada. In this case, the deer totally avoided browsing, as determined by observations on their feeding. The islands with the black-tailed deer had greater density, cover, and diversity of bryophytes than the islands with no deer. This presumably is due to reduced competition with tracheophytes for light and the total avoidance of foraging on bryophytes by the black-tailed deer.



Figure 75. *Odocoileus hemionus sitkensis*, Sitka Deer, at Haida Gwaii, Vancouver Island, Canada. Photo by D. Gordon E. Robertson, through Creative Commons.



Figure 76. *Odocoileus hemionus sitkensis*, a subspecies found on Vancouver Island, Canada. Photo by Wanetta Ayers, through public domain.

### Reindeer/Caribou – *Rangifer tarandus*

Reindeer and caribou (*Rangifer tarandus*; Figure 77) are different names for the same ungulate in different parts of the world. Their browsing on lichens, especially those

known as reindeer "mosses" (*Cladina* spp.; Figure 78), is well known (Väre *et al.* 1995; Olofsson *et al.* 2004), but their consumption of bryophytes is less well understood.



Figure 77. *Rangifer tarandus* (caribou) grazing. Photo by Peter Nijenhuis, through Creative Commons.



Figure 78. *Cladina* spp. in Tyresta National Park, Sweden – preferred food of reindeer. Photo by Peder Curman, through Creative Commons.

### Importance of Mosses in Diet

Several authors claim that reindeer/caribou seldom eat mosses, despite the limited availability of other foods (Person *et al.* 1980; White & Trudell 1980; Olofsson *et al.* 2004). In a study of food preferences in northern Sweden, Danell *et al.* (1994) found that these animals had a high preference for lichens in winter, but a low one for the common moss *Pleurozium schreberi* (Figure 79). The researchers were unable to explain this difference by nitrogen content, organic matter digestibility, or fiber.





Figure 79. *Pleurozium schreberi*, a common moss often avoided by reindeer and caribou. Photo by J. C. Schou, with permission.

Crête *et al.* (1990) compared lactating caribou in two tundra habitats (Figure 80), one where lichens occupied more than 50% of the ground cover and one where mosses, bare soil, and graminoids dominated the vegetation. The rumen contents reflected the differences in the two habitats. Fewer lichens were eaten in the habitat dominated by mosses and graminoids. Nevertheless, selection for lichens was intense, with lichen cover 25X less but only 1.5-2X less abundant in the rumina.



Figure 80. Barren-ground caribou (*Rangifer tarandus groenlandicus*) grazing in the tundra. Photo from USFWS, through public domain.

Klein (1979) found that the Peary caribou (*Rangifer tarandus pearyi*; Figure 6, Figure 82) – a subspecies in the high Arctic islands of Canada's Nunavut and Northwest territories – eat a smaller percentage of lichen than do caribou on the mainland. Rather, they rely on vascular plants and a greater quantity of mosses. Rumen contents contained an average of 58% mosses in Peary caribou of five regions of the Canadian Arctic archipelago during winter, representing five regions (Thomas & Edmonds 1983). Nevertheless, they still prefer the rather scarce foliose lichens in winter (Klein 1979).

In Arctic ecosystems (Figure 81), tracheophyte food can be scarce and mosses subsequently form a major component of the diet of many vertebrate herbivores. In addition to the rodents and birds already discussed in earlier chapters as bryophyte herbivores, ruminants in the Arctic also depend on mosses as a component of their diet. These include reindeer and caribou (*Rangifer tarandus*; Figure 80-Figure 82) and muskox (*Ovibos moschatus*; Figure 83) (Prins 1982; Prop & Vulink 1992; Longton 1997; van der Wal *et al.* 2000; Joly *et al.* 2007).



Figure 81. Arctic tundra from air. Photo by Robert Berdan, with permission.



Figure 82. *Rangifer tarandus pearyi*, a moss eater. Photo by Morgan Anderson, Environment, with online permission.



Figure 83. Muskox (*Ovibos moschatus*), a tundra moss eater. Photo through Creative Commons.



Manseau *et al.* (1996) considered the habitat of caribou (*Rangifer tarandus*; Figure 80) to be very susceptible to both grazing and trampling by the caribou. In fact, it appears that the herd size is regulated by the amount of available forage in its summer range. They found that the lichen mat was absent in grazed areas of the shrub tundra and that those areas were either bare or occupied by fragments of dead lichens and mosses.

On the other hand, lichens are very important to the caribou diet. Pharo and Vitt (2000) reported that in the montane forests of western Canada, the lichens preferred by the endangered woodland caribou (*Rangifer tarandus caribou*; Figure 84) were abundant, but the ground cover was dominated by feather mosses, especially *Pleurozium schreberi* (Figure 79).



Figure 84. Caribou (*Rangifer tarandus caribou*) feeding in tundra, Northwest Territories, Canada. Photo by Robert Berdan, with permission.

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) includes coprophagy among its feeding strategies (van der Wal & Loonen 1998). That is, they feed on the feces of barnacle goose (*Branta leucopsis*; Figure 85). In fact, the majority of the reindeer in the research area were seen feeding on these droppings instead of vegetation. The number of goose droppings eaten were enough to supply the daily energy requirements for 68 reindeer. But they were very selective in their choice of droppings, choosing those containing grass and avoiding those with moss fragments. There did not appear to be important differences in nitrogen, phosphorus, magnesium, calcium, sodium, potassium, or energy content between the two types of feces. Fiber, on the other hand, differed between grass- and moss-dominated droppings, with less fiber associated with the mosses. Thus, the grass-dominated droppings were more digestible.

Nevertheless, Arctic herbivores, including *Rangifer tarandus*; Figure 80, Figure 84), do consume substantial quantities of bryophyte biomass (van der Wal & Brooker 2004) and further damage them through trampling. Liddle (1997) has shown that trampling can be particularly destructive to mosses in Arctic ecosystems because of their slow growth rate and recovery (Callaghan *et al.* 2001).



Figure 85. Barnacle Geese (*Branta leucopsis*); Svalbard reindeer eat the feces of this goose, but avoid feces with mosses. Photo by Allan Hopkins, through Creative Commons.

### Digestibility

Several authors have attributed the usual lack of consumption to the low digestibility of mosses (Person *et al.* 1980; White & Trudell 1980; Thomas & Kroeger 1981). Nevertheless, on Arctic islands with little lichen availability, the caribou herds eat mosses (Staland *et al.* 1979).

Robert Pegau, in correspondence with Howard Crum, reported that reindeer in Alaska scarcely digest mosses (Crum 1973), although they do graze on *Polytrichum* (Figure 5), *Aulacomnium turgidum* (Figure 86), and *Hylocomium splendens* (Figure 87) (Bland 1971). A high content of moss (up to 12%) in winter in the rumen of reindeer at Hardangervidda, Norway, may be ingested unavoidably while grazing on lichens (Gaare & Skogland 1975). Lichens, on the other hand, are readily digested (Crum 1973).



Figure 86. *Aulacomnium turgidum* in Norway, a moss species eaten by Alaskan reindeer. Photo by Jutta Kapfer, with permission.





Figure 87. *Hylocomium splendens*, a moss species eaten by Alaskan reindeer. Photo by Rob Routledge, through Creative Commons.

Nevertheless, when lichens are overgrazed, reindeer may turn to mosses. On Svalbard, where desirable lichens are scarce, Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) had a rumen content of 32-39% mosses, hardly an accidental accompaniment to lichens (Reimers 1977). In fact, van der Wal (2006) considers Svalbard reindeer to be moss specialists, consuming up to 54% of their winter diet as mosses, a figure similar to that of Peary caribou (*Rangifer tarandus pearyi*; Figure 6, Figure 82) in northern Canada (Klein 1979). Rather than eating lichens, reindeer in the High Arctic seem to have replaced lichens as winter forage with bryophytes (Staalnd *et al.* 1983; Staalnd 1986; Longton 1997). Staalnd *et al.* (1983) found that the mosses on Svalbard provided a higher mineral content than the food available in Norway, but at the same time, the mosses had lower digestibility than the lichens and browse in Norway.

In a different study, Bjorkvoll *et al.* (2009) found that the winter diet of Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) was only 22-30% mosses during the three-year period of the study. Effects of snow cover in late winter affected the dietary composition. *Polytrichum* (Figure 5) was the most common bryophyte and comprised a relatively high proportion in the early winter diet.

In the southern Northwest Territories, Canada, the barren-ground caribou (*Rangifer tarandus groenlandicus*; Figure 1, Figure 88) included mosses, lichens, and shrubs in its diet (Thomas *et al.* 1984). Using fermentation in ruminal fluids in test tubes, Thomas and coworkers found that the dry matter biomass of shrubs was reduced by 37-51%, whereas the bryophytes were reduced only 7-28%. The lichens averaged 49% reduction in 180 hours. In a different case, Thomas and Kroeger (1981) examined *in vitro* digestion in ruminal fluids from *Rangifer tarandus groenlandicus* that had been shot in its winter range in southern Northwest Territories, Canada. This animal had poor digestion (15-27%) of two species of mosses and a liverwort.

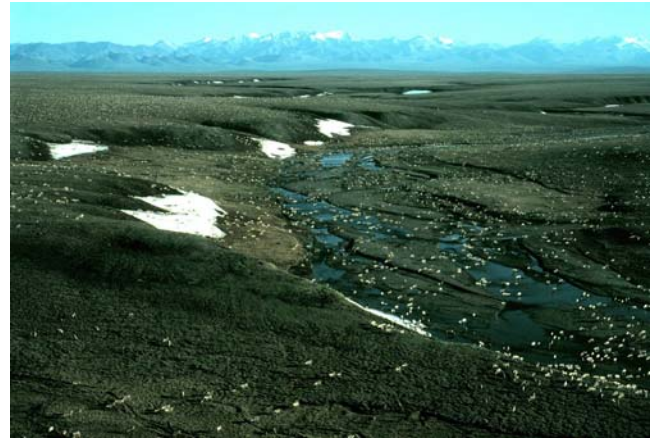


Figure 88. Barren-ground caribou (*Rangifer tarandus groenlandicus*) herds. Such numbers cause considerable damage to the vegetation, including bryophytes. Photo from U.S. Fish and Wildlife, through public domain.

In Aoluguya, Great Khingan Mountain Range of Inner Mongolia, Feng and Bai (2011) examined factors related to bryophyte consumption and digestion. The bryophytes have high concentrations of acid-detergent fiber, making them indigestible. This raises the question, what permits some reindeer to subsist largely on bryophytes, especially in winter?

Staalnd and coworkers (1979) suggest that the reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) on Svalbard may be adapted to eating mosses. These reindeer have an enlarged caecum-colon complex that appears to be an adaptation to a bryophytic diet by using the assistance of bacteria. These reindeer also have a high number of fiber-digesting rumen bacteria (Orpin *et al.* 1985), facilitating digestion. The rumen bacteria of the Svalbard reindeer are very effective in facilitating fiber digestion and nitrogen metabolism, providing an important adaptation for living in high Arctic habitats with poor nutritional conditions.

The Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) eat mosses in the winter because they are unable to migrate to forested lichen habitat (Longton 1992). Nevertheless, digestibility of mosses by these caribou is typically low, only 11-35% in summer and 3-11% in winter (Thomas & Kroeger 1980). Thus, one must ask just what the mosses provided for the animals. If ruminants, with their massive digestive bacteria flora, are unable to digest the mosses, one would assume they would be even less digestible for most other large mammals. There are likely to be other populations with similar winter grazing problems. Callaghan *et al.* (2004) considered deep snow to be a deterrent from winter grazing in some Arctic areas in some years. Areas of deep snow could force these ruminants into lower elevations or lower latitudes and prevent them from finding enough of the desired winter food source of lichens.

If mosses are difficult to digest and provide limited nutritional value, why are they heavily consumed in the Arctic? Ardea and Sage (1982) claim that the reindeer must consume 7 kg of mosses to extract the same energy they would get from just 0.5 kg of tundra grass.

We have seen that Prins (1982) suggested that they eat mosses for their arachidonic acid because of its ability to remain flexible in winter. These acids are major constituents of animal fats, especially in phospholipids of



cell membranes (Ardea & Sage 1982). These make the membranes more fluid, especially at the low temperatures of winter.

Feng and Bai (2011) added to the arachidonic acid possibilities. Reindeer are not able to synthesize arachidonic acid, but that which is ingested can provide several benefits to them. This acid is a precursor for some prostaglandin hormones, it has a low melting point that could lower the freezing point of the reindeer extremities, and it provides protection to cell membranes in the cold.

### Effects on Soil Temperature

In the wet meadow vegetation of Barrow, Alaska, USA, Miller *et al.* (1980) found that in exclosures (Figure 74) the moss increased and the thaw depth decreased, suggesting that the mosses insulated the permafrost (Figure 89) against warming, and thus against thawing. Van der Wal and Brooker (2004) examined effects of reindeer herbivory on a moss layer of *Sanionia uncinata* (Figure 90), *Tomentypnum nitens* (Figure 91), and *Aulacomnium* spp. (Figure 92). Moss depth in the grazed controls was  $38 \pm 6$  mm compared to  $57 \pm 10$  mm in the ungrazed exclosures. Furthermore,  $\text{NH}_4\text{-N}$  was considerably lower inside the exclosures, but nitrogen mineralization potential was reduced by greater moss depth. A 10-cm-thick mat of mosses causes  $\sim 4.4^\circ\text{C}$  drop in soil temperature, with the temperature decreasing with moss depth (Figure 93). Manipulating the soil temperature had no effect on moss growth, but the grass *Poa arctica* and flowering plant *Cardamine nymanii* (Figure 94) both were reduced by 50% biomass in the chilled soils (van der Wal *et al.* 2001). These temperature decreases not only affect roots and rhizomes of tracheophytes, but they also affect decomposer communities by affecting the soil microbes and consequently affecting nutrient cycling (Harrison & Bardgett 2008).



Figure 89. Digging in permafrost in the tundra, using a jackhammer. Photo by Nick Bonzey, through Creative Commons.



Figure 90. *Sanionia uncinata*, a moss species affected by reindeer grazing. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 91. *Tomentypnum nitens*, a moss species affected by reindeer grazing. Photo by Scot Loring, through Creative Commons.



Figure 92. *Aulacomnium palustre*, a moss species affected by reindeer grazing. Photo by Kristian Peters, through Creative Commons.



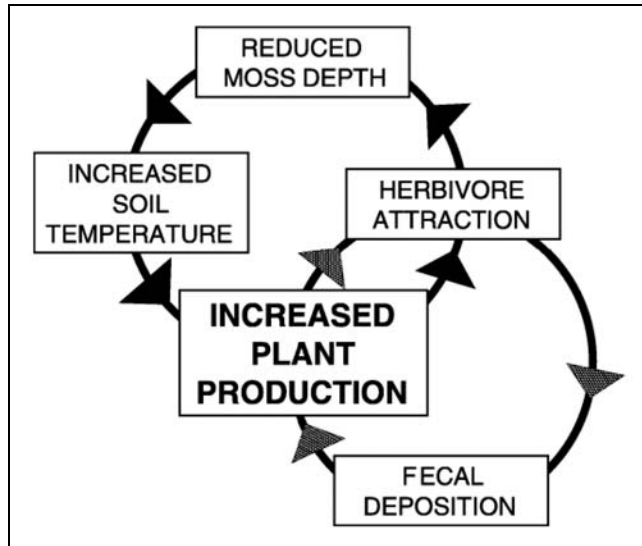


Figure 93. Relationship of mosses, herbivores, and soil temperature as conceptualized by van der Wal and Brooker 2004.



Figure 94. *Cardamine nymanii* in flower in Spitzbergen, a food much eaten by ruminants in Alaska. Photo by Bjoertvedt, through Creative Commons.

### Microbial Responses to Grazing

Väre *et al.* (1996) found that microbial activity was significantly depressed at sites grazed by reindeer. This seems to be the result of reduced soil moisture at the grazed sites, especially during dry periods. Furthermore, grazing reduced the levels of all exchangeable nutrients by 30-60% in the organic layer of the soil. These factors contributed to the reduction of fine roots.

### Temporal Differences

Both food choice and digestibility vary by season. Thomas and Kroeger (1980) found summer digestibility of mosses to range 11-35%, whereas winter digestibility ranged only 3-11%.

Thompson and McCourt (1981) studied the phenology of diet in the porcupine caribou herd (*Rangifer tarandus granti*; Figure 95) in the northern Yukon. The winter diet was dominated by lichens (66.7%) with most of the remainder being mosses (28.8%). In summer they shifted to primarily tracheophytes, especially sedges in spring, but shrubs dominated (>98%) after calves were born. The diet of shrubs declined and lichens again became prominent beginning in August.



Figure 95. Porcupine caribou (*Rangifer tarandus granti*) grazing. Photo by Dean Biggins, through public domain.

In the Great Khingan Mountain Range of Inner Mongolia, bryophyte consumption by reindeer also varied by season (Feng & Bai 2011). In April bryophytes comprised 5.63% of the feces, dropping to 2.2% in June, and rising to 12.9% in September. The four most common genera of bryophytes were *Pleurozium* (Figure 79), *Dicranum* (Figure 11), *Aulacomnium* (Figure 86, Figure 92), and the leafy liverwort *Ptilidium* (Figure 96). *Pleurozium schreberi* (Figure 79) comprised over 70% of the bryophyte total. But some seasonal differences are present. *Polytrichum juniperinum* (Figure 97) only occurred in large amounts in September. Despite the seasonal changes in amount of bryophytes eaten, the relative proportions among the other bryophyte species did not change appreciably between seasons. Nevertheless, sampling of the dominant forest floor bryophytes revealed that the reindeer are selective. *Hylocomium splendens* (Figure 87), *Sphagnum* spp. (Figure 98), and *Pleurozium schreberi* (Figure 79) are dominant bryophytes in the four types of forests investigated, but of these only *Pleurozium schreberi* was eaten. Additionally, *Didymodon* (Figure 99) and *Racomitrium* (Figure 100) occurred only occasionally in the feces.



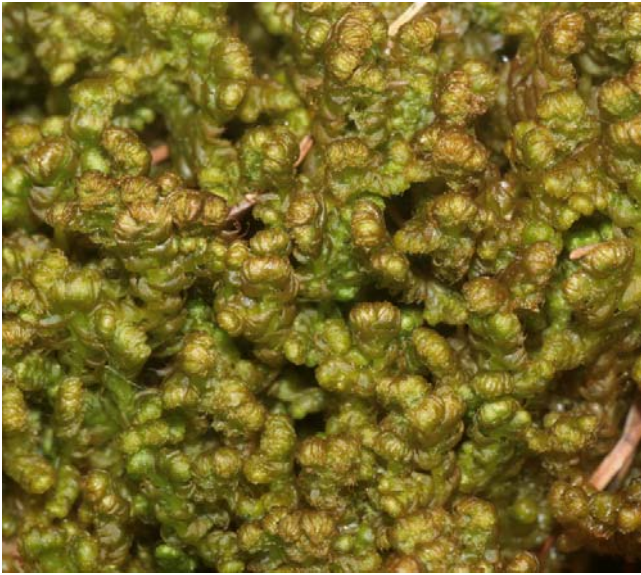


Figure 96. *Ptilidium ciliare*, leafy liverwort in a genus that is one of the four most common bryophytes in the reindeer grazing grounds of the Great Khingan Mountain Range of Inner Mongolia. Photo by Hermann Schachner, through Creative Commons.



Figure 97. *Polytrichum juniperinum*, a moss species that occurred in its greatest amounts in reindeer feces in September in the Great Khingan Mountain Range of Inner Mongolia. Photo by Janice Glime.



Figure 98. *Sphagnum austini*, a dominant moss in Mongolian reindeer habitats, but was not eaten by them. Photo by Michael Lüth, with permission.



Figure 99. *Didymodon rigidulus* var *icmadophilus*, member of a genus that is occasionally consumed by reindeer in the Great Khingan Mountain Range of Inner Mongolia. Photo by Michael Lüth, with permission.



Figure 100. *Racomitrium* in grey-green mounds, a genus that occasionally is consumed by Mongolian reindeer. Photo by Manfred Morgner, through Creative Commons.

In the five regions studied, Thomas and Edmonds (1983) found that monocots and mosses comprised 13% and 58%, respectively, of the rumen content of Peary caribou (*Rangifer tarandus pearyi*; Figure 6) in the Canadian Arctic archipelago. However, the digestibility of mosses for caribou is low, with the summer digestibilities of mosses ranging 11-35%, whereas lichens range 18-86% (Thomas & Kroeger 1980, 1981). In winter the mosses drop to 3-11% digestibility, suggesting they are not being consumed primarily for their nourishment. Perhaps it fools the caribou into "thinking" that they are full.

Thomas *et al.* (1984) also found that the dry matter disappearance of 22 plant species was significantly higher in March of 1981 than in tests performed one year earlier. The variation in the ruminal fluids coincided with differences in the physical condition of the caribou, which may have resulted from their nutritional history.

#### Site Differences

Based on these observations, we can expect the diet to differ by location. Pearce (1997) found that in the Kara area of Russia, 14% of the moss sites and 10% of the lichen sites experienced severe damage from reindeer activity. On



the other hand, in Norway, 73% of the moss sites and 85% of the lichen sites suffered from grazing and trampling. The reindeer populations of Norway had doubled in the previous years, resulting in soil erosion in 75% of the sites. Only 8% of the Russian sites suffered from erosion.

Sørmo *et al.* (1999) examined fragments in the rumen of Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7) in the western parts of Spitsbergen at Nordenskiöld where tundra vegetation is somewhat abundant and on the island of Nordaustlandet where they live in a polar desert with scarce vegetation. On Nordenskiöld the rumen contents were primarily mosses and grasses, whereas on Nordaustlandet they were primarily the flowering plants *Saxifraga* spp. (Figure 101).



Figure 101. *Saxifraga cespitosa* on Svalbard. This genus is the primary food of the Svalbard reindeer on Nordaustlandet. Photo by Victor M. Vicente Selvas, through Creative Commons.

### Grazing Effects on Bryophytes and Vegetation

Van der Wal (2006) considered the ruminant herbivores to cause predictable changes in the ecosystem vegetation. Van der Wal points out that reindeer can deplete the lichens and switch to mosses (Staaland *et al.* 1993) with no detrimental effects to the reindeer population (Cooper & Wookey 2001). In fact, the carrying capacity for large ungulates increases when the vegetation switches to mosses, and increases again when it converts to grasses after extensive herbivory on mosses. A similar succession from lichens to mosses to graminoids is known where caribou (reindeer) range in Greenland (Thing 1984), Russia (Vilchek 1997), North America (Palmer & Rouse 1945; Klein & White 1987; Manseau *et al.* 1996), Fenno-Scandia (Helle & Aspi 1983, Gaare 1997), and the high arctic islands (Van der Wal *et al.* 2001). Even domesticated reindeer in boreal forest ecosystems cause the conversion of lichen vegetation to mosses (Väre *et al.* 1996; Mäkipää 1998). And in Norway the moss-dwarf shrub heath gives way to grass domination under the pressure of reindeer grazing (Olofsson *et al.* 2001, 2004). Thing (1984) interpreted this progression of species as ecosystem damage.

Sarvas (1937) found that mosses like *Polytrichum juniperinum* (Figure 97) can survive feeding and trampling because they have rhizomes and rhizoids that can survive

the above-ground feeding. These underground parts are able to germinate and form new plants. Oksanen (1978) found that *Polytrichum hyperboreum* (Figure 102) in northern Norway is very resistant to trampling by reindeer. It is likely that *Polytrichum* species are also dispersed by the reindeer, and some of these are delivered to areas where competition with species of *Cladonia* (Figure 103) is avoided (Helle & Aspi 1983).



Figure 102. *Polytrichum hyperboreum* with capsules, a moss species that is very resistant to trampling. Photo by Kristian Hassel, through Creative Commons.



Figure 103. *Cladonia cornuta*, a member of the lichen genus that competes with the moss *Polytrichum*. Photo through Creative Commons.

Van der Wal (2006) suggests the change in species begins with selection of lichens over mosses, causing greater lichen losses. This change is further promulgated by trampling, which is more damaging to lichens than to mosses, especially when they are dry (Cooper *et al.* 2001). If grazing is suppressed, the system may change back to lichen domination, but the change is slow (Crettenden 2000; Cooper & Wookey 2001; Den Herder *et al.* 2003). In fact, as lichens recover, they may "smother" the mosses (Gaare 1997; Van der Wal *et al.* 2001). A more likely explanation is the allelopathic effect of the many lichen secondary compounds (Lawrey 1995).

In *Pinus sylvestris* forests (Figure 104) of Fennoscandia, in 50-year-old exclosures indicate that



certain bryophytes benefit from reindeer grazing (Väre *et al.* 1995). This was particularly true for *Dicranum* spp. (Figure 11) and *Pleurozium schreberi* (Figure 79). In heavily grazed sites, the food lichen species *Cladina* spp. (reindeer "moss"; Figure 78) disappears. However, in ungrazed sites, *Cladina* species replace the *Cladonia* (Figure 103) lichen species and small bryophytes like *Barbilophozia* spp. (Figure 105), *Pohlia nutans* (Figure 106), and even *Polytrichum* spp. (Figure 102).



Figure 104. *Pinus sylvestris* (Scots pine) forest with mosses. Photo by Hermann Falkner, through Creative Commons.



Figure 105. *Barbilophozia floerkei*, a leafy liverwort among the species replaced by *Cladina* in ungrazed sites. Photo by Hermann Schachner, through Creative Commons.



Figure 106. *Pohlia nutans* in Svalbard, among the moss species replaced by the lichen *Cladina* in ungrazed sites. Photo by Michael Lüth, with permission.

Virtanen (2000) used exclosures to determine the effects of herbivory on vegetation of a mountain snowbed in northwestern Finland. Unlike Sarvas (1937) and Oksanen (1978), Virtanen found that the dead plant material of *Polytrichaceae* (Figure 97, Figure 102) in the 15-year exclosures had increased; the moss *Kiaeria* (Figure 107) had disappeared. His results contradicted the assumption of other researchers that herbivory was unimportant in areas of low productivity. In these snowbeds, it clearly had an impact.



Figure 107. *Kiaeria starkei*, a moss species that disappears in exclosures. Photo by Hermann Schachner, through Creative Commons.

Olofsson *et al.* (2001) examined the effects of summer grazing on the tundra heath vegetation in northern Norway. Comparing winter grazed, lightly summer grazed and heavily summer grazed vegetation at four different sites. They concluded that the highest productivity occurs at intermediate grazing pressure. They found that intensive grazing may be responsible for the transition from a moss-rich heath tundra to a productive grass-sedge-dominated steppe-like tundra vegetation. Intermittent grazing can actually enhance summer productivity.

In the sub-Antarctic on South Georgia, experimental reindeer exclosures demonstrated the changes to the vegetation after 1 year (Leader-Williams *et al.* 1987). Native grasses (*Poa flabellata*; Figure 108) and dwarf shrubs (*Acaena magellanica*; Figure 109) increased in response to the absence of grazing. The moss *Polytrichum* (Figure 97, Figure 102) likewise increased, but to a lesser extent. This is reminiscent of the responses in rodent exclosures (see Chapter 17). Macrolichens showed little change, as did moss-bank communities. The lichen cover is likely to require decades to recover.

Using approximately 3000 permanent plots in Finland and more than 10,000 plots in all in three different surveys, Mäkipää and Heikkinen (2003) measured changes in the vegetation. During this time, the forest floor moss *Hylocomium splendens* (Figure 87) decreased in abundance while *Dicranum polysetum* (Figure 110) increased. In the northern part of Finland, grazing by semi-domestic reindeer coincided with a decline of *Cladina* (Figure 78) lichens, a favorite food, while the mosses *Dicranum* spp. increased. *Polytrichum juniperinum* (Figure 97), *Pohlia nutans* (Figure 106), and *Brachythecium* sp. (Figure 113), moss species typical of disturbed sites, increased. *Sphagnum* (Figure 98)



abundance decreased, especially in western Finland where the moss *Pleurozium schreberi* (Figure 79) also was favored.



Figure 108. *Poa flabellata* on South Georgia, a species that increases when grazing stops. Photo by Roger Key, with permission.



Figure 109. *Acaena magellanica*, a shrub that increases when grazing is stopped. Photo by El Grafo, through Creative Commons.



Figure 110. *Dicranum polysetum*, a moss species that increased in permanent plots. Photo by Hermann Schachner, through Creative Commons.

Hansen *et al.* (2007) followed vegetation changes for 26 years following the reintroduction on the northwest coast of Spitsbergen, Svalbard, of the Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Figure 7). The population size fluctuated, and when it reached high numbers, it caused a top-down effect on the vegetation that included a decrease in the cover of mosses. The preferred winter forage, fruticose lichens, almost disappeared. When the grazing pressure was relieved, the mosses not only recovered completely, but within six years they exceeded the pre-reindeer levels.

In the Arctic and alpine tundra, reindeer (*Rangifer tarandus*; Figure 77) consume 22-30% of their winter diet as moss (Heggberget *et al.* 2010). These researchers expressed concern that climate change, predictably greater in these northern areas, could compromise the available winter forage. Lichens are likely to be impacted, forcing the reindeer to seek other forage. In some populations, a larger alimentary tract has adapted to the reindeer diet.

### Roe Deer – *Capreolus capreolus*

Several studies have revealed the ability of hoofed mammals to transport bryophyte propagules. One such study demonstrated the **epizoochorous** dispersal of bryophyte fragments by roe deer (*Capreolus capreolus*; Figure 111) (Heinken *et al.* 2001). They found 106 bryophyte fragments, almost all stem fragments, lodged in the coats and hooves of 15 roe deer and 9 wild boar (*Sus scrofa*; Figure 112). These represented 12 bryophyte species, with the most abundant being *Brachythecium velutinum* (Figure 113), *Hypnum cupressiforme* (Figure 4), and *Eurhynchium hians* (Figure 114). These were typically about 3.6 mm long, but ranged 0.5-35 mm. The species that were most common were slender pleurocarpous mosses (growing horizontally) with erect, acute leaves. Robust acrocarpous mosses (growing upright) that formed tall turfs were generally absent.



Figure 111. Roe deer (*Capreolus capreolus*) male and female, showing the hooves that can transport bryophyte fragments. Photo by Jojo through Wikimedia Commons.

Roe deer can do considerable damage to bryophyte vegetation (Clément & Touffet 1981). Following fire in the Brittany heathlands, roe deer were responsible for bryophyte disappearance due to scraping by roe deer.





Figure 112. Wild boar (*Sus scrofa*), a species that can transport bryophytes in its long hair and on its hooves. Photo by Jerzy Strzelecki, through Creative Commons.



Figure 113. *Brachythecium velutinum*, a moss that is one of the most abundant bryophytes transported by sheep. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 114. *Eurhynchium hians*, one of the most abundant moss species carried by roe deer (*Capreolus capreolus*). Photo by Michael Lüth, with permission.

Bryophytes do not appear to serve as food for this species (Tixier *et al.* 1997). Although they are generalist feeders by using a variety of types of food, they are selective within the food types. Their use of food species correlates negatively with fiber content. Bryophytes were specifically avoided in all seasons. Even so, they preferred plants that had high concentrations of protein-binding

phenolic compounds, leading Tixier and coworkers to suggest that they might have specific mechanisms for deactivating these compounds. For many animals, protein-binding compounds prevent the animals from obtaining nutrition from the proteins they eat, even from accompanying foods that don't have the binding compounds.

### Hog Deer – *Axis porcinus*

In southeastern Australia, both introduced mammals and native species consume plants (Davis *et al.* 2008). Whereas the swamp wallabies (*Wallabia bicolor*; Figure 115) consume the largest proportion of tree browse, the hog deer (*Axis porcinus*; Figure 116) consume the largest proportion of mosses, however only removing less than 0.01%.



Figure 115. *Wallabia bicolor* and large joey. Photo by Peripatus, through Creative Commons.



Figure 116. *Axis porcinus*, a moss consumer. Photo by Brent Huffman, through Creative Commons.

### Summary

Bryophytes and ruminants interact in various ways. Some of these animals eat the bryophytes, particularly reindeer in Arctic regions, and most are capable of creating disturbance that can damage the bryophytes. Trampling and scraping break and dislodge the



bryophytes, but at the same time these activities can contribute to dispersal as the fragments adhere to hooves and fur/hair/wool.

Reindeer/caribou (*Rangifer tarandus*) typically cannot digest bryophytes well, but on Svalbard, where they have no place to go for winter, mosses are a staple in the diet. They seem to have adapted by being able to absorb more of the nutrients from the mosses through an enlarged caecum-colon complex.

Both black-tail (*Odocoileus hemionus*) and white-tail (*Odocoileus virginianus*) deer and roe deer (*Capreolus capreolus*) apparently avoid eating bryophytes.

When grazing is light, it can favor such mosses as *Rhytidiadelphus squarrosus*, *Polytrichaceae*, and *Brachythecium*. Colonizers like *Pohlia nutans* can benefit from disturbance and increased light. Leafy liverworts like *Barbilophozia floerkei* decrease with grazing. But the bryophyte communities depend on the site, with Arctic and alpine communities responding differently from more temperate ones. Rodents likewise can have a profound effect on the bryophytes, with communities responding differently depending on the foraging ruminants present.

Bryophytes suffer from manuring and urine, perhaps due to increased microbial decomposition, or to greater competition from the enriched tracheophytes.

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