CHAPTER 17-3
RODENTS AND BATS – NON-MUROIDEA

TABLE OF CONTENTS

CHAPTER 17-3
RODENTS AND BATS – NON-MUROIDEA

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

Soricomorpha

Soricidae – Shrews

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

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

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

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

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

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

Sorex cinereus – Long-tailed Shrew

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

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

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

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

Sciuromorpha

Sciuridae

Records indicating that squirrels use mosses to line their nests are old (Tripp 1888). But sometimes, the mosses use squirrel activity to their advantage (Ken Adams, Bryonet 30 April 2020). In the Epping Forest, UK, ***Zygodon viridissimus*** competes with ***Z. forsteri*** for space on the grooves created by squirrel gnawing. The former often out-competes the latter.

Tamias merriami – Merriam Chipmunk

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

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

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

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

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

Tamiasciurus hudsonicus – American Red Squirrel

The American red squirrel (***Tamiasciurus hudsonicus***; Figure 14) seems to eat just about anything. It is more tame than most squirrels, and I have even had a confused squirrel climb my leg! It also seems to like decorating its abode, using paper, moss, and other local objects it can find (Hanrahan 2012).

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

Sciurus vulgaris – Eurasian Red Squirrel

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

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

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

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

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

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

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

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

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

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

Sciurus carolinensis – Grey Squirrel

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

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

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

Spermophilus parryii – Arctic Ground Squirrels

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

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

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

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

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

Glaucomys – Flying Squirrels

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

Glaucomys sabrinus – Northern Flying Squirrel

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

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

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

Glaucomys volans – Southern Flying Squirrel

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

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

Lagomorpha – Hares, Rabbits, and Pikas

Leporidae – Rabbits and Hares

Lepus arcticus – Arctic Hare

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

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

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

Oryctolagus cuniculus – European Rabbit

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

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

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

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

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

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

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

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

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

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

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

But rabbits (***Oryctolagus cuniculus***; Figure 28) can also create habitat for bryophytes. Callaghan (2015) reports that some mosses thrive due to grazing activities by rabbits in the UK. A more spectacular find occurred at an old tin works in Cornwall, where the rare copper moss ***Scopelophila cataractae*** (Figure 37) benefits by the creation of habitats by rabbits. As succession proceeds on the exposed mineral soil, the tracheophytes replace the bryophytes. However, when the rabbits arrive, the rabbits create a network of runways and tunnels, exposing the metal-rich soil where the copper moss thrives. These serve as refugia for this moss species that is disappearing as the more coarse vegetation develops. The entrances to burrows are clothed in a mat of protonemata (Figure 38) that have abundant gemmae (Figure 39). Callaghan speculates that the rabbits must disperse thousands of these gemmae on their fur, and the entrance to the tunnel is often the benefactor substrate.

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

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

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

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

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

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

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

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

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

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

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

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

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

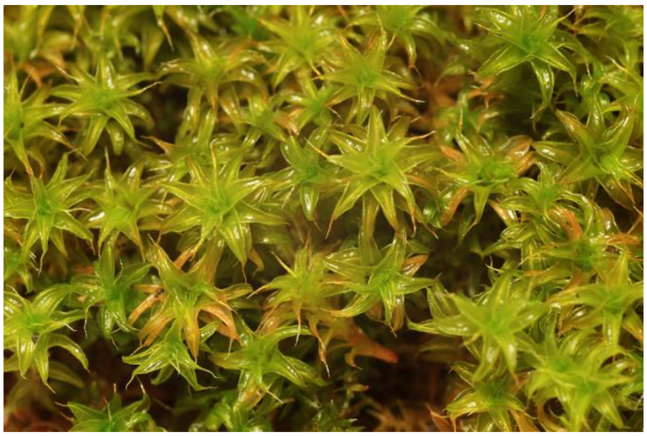

Figure 48. ***Syntrichia ruralis*** ssp ***ruralis***, a moss that declined when rabbit populations declined. Photo by Barry Stewart, with permission.

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

The results of Ranwell (1960) differ somewhat from those of Watt (1957), who showed that disappearance of rabbits resulted in the decrease of mosses in ungrazed pasture over long periods of time. Watt found 29 bryophyte species, but ***Rhytidiadelphus squarrosus*** (Figure 42) is found only in the ungrazed community. This is in contrast to its common presence in grazed pasture on the South Downs and other locations in Breckland, England. On the other hand, 11 species occur exclusively in the grazed area. These are all small and 10 of the 11 are acrocarpous. As in the Ranwell (1960) study, Watt found that mosses in the ungrazed turf are tall and mostly pleurocarpous. The small mosses seem to be unable to survive competition with taller vegetation, including competition for light. The larger mosses, on the other hand, seem to thrive in the ungrazed conditions. Watt considered these results to support the hypothesis that "in the grazed community the competitive power of the potentially taller growing plants is reduced by grazing sufficiently to allow the smaller species to survive and that in the ungrazed the unchecked growth of taller growing species eliminates or tends to eliminate the smaller, whether they are annual or perennial of varied life-forms."

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

Ochotonidae – Pikas

Ochotona princeps – American Pika

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

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

The presence of pikas is usually a good indicator of regions with rocky, mesic, cool habitat (Figure 51) with long winters and short summers (Simpson 2009). Although the American pikas (***Ochotona princeps***; Figure 51) are a high elevation species in western North America, in the Columbia River Gorge they live near sea level (Horsfall 1925; Varner & Dearing 2014a, b). But at low elevations in the southern part of the Columbia River Gorge, Oregon, USA, the known temperature range was extended and the long winters and typical snow accumulation were not present.

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

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

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

Varner and Dearing (2014b) supported this assessment, finding that the moss cover insulates the interstices of the talus slopes from temperature fluctuations. Varner and Dearing (2014a) speculated that the mosses could cool the microclimates of the talus in the valley (Figure 51), making the climate suitable for the pikas. The pikas are able to travel long distances beneath the thick moss cover. Even their extensive moss consumption only removes about 0.002% of the moss in their home ranges in one year. Hence, unlike the lemmings, the pikas can enjoy the cover of the mosses without the danger of eliminating it.

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

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

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

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

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

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

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

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

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

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

Ochotona collaris – Collared Pika

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

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

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

Like ***Ochotona principes*** (Figure 50-Figure 54), ***O. collaris*** (Figure 55) can run across the talus slope under the moss cover (Morrison *et al*. 2004) in its Yukon, Canada, home (Morrison *et al*. 2009). This most likely reduces predation risk as well as modulating the temperatures they experience (Morrison *et al*. 2004). Nevertheless, choice of food nutrition level does not seem to be dictated by predation risk. On the other hand, in experiments total amount of forage removed by the pikas was inversely related to predation risk.

Erinaceidae – Hedgehogs

The European hedgehog (***Erinaceus europaeus***) is a nocturnal species of Europe and Central Asia. As its name inplies, it is common in hedgerows. The hedgehog (***Erinaceus europaeus***; Figure 56) is the only British mammal to have spines (Wildscreen 2010). They have fairly short tails, long legs, and small ears. They eat mostly insects, but may include other small animals, like frogs and rodents.

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

When young hedgehogs are born, they have a coat with soft, white spines under the skin to protect the mother during birth. After a few hours these emerge. After about 36 hours, a second coat of dark-colored spines emerges, then later a third set emerges. By day eleven, the hedgehogs are able to curl into a ball, and finally after 14 days their eyes open. They are nocturnal, having large eyes, but they may also be active in the daytime (Wikipedia 2017a). They are solitary animals, and only the female takes care of the young.

They rest in the daytime in nests made of twigs, leaves, grass, pine needles, and other foliage. The "other foliage" includes mosses (Figure 57), sometimes in large quantities! Fortunately, the nest is re-used by another individual. The hedgehog selects pleurocarpous mosses that are available near the nest among its nesting materials (van Laar & Dirkse 2010). The authors suggest that the mosses may be selected to maintain a suitable humidity in the nest.

Figure 57. ***Erinaceus eupopaeus***, hedgehog, carrying moss, presumably for a nest. Photo through Creative Commons.

CHIROPTERA – Bats

Pteropidae – Flying Foxes

Pteropus conspicillatus – Spectacled Flying Fox

The flying fox of Australia is really a kind of bat associated with the rainforest habitats of the Wet Tropics bioregion of northeastern Queensland, Australia (Parsons *et al*. 2007). The spectacled flying fox (***Pteropus conspicillatus***; Figure 58-Figure 59) seems like an unlikely candidate for eating mosses, but... this bat ingests mosses, as evidenced by feces (**splat**) comprised of 14% moss (Andi Cairns, pers. comm. 4 December 2004). Samples from the wet complex notophyll vine forest had the greatest occurrence of bryophytes in fecal samples (22.8% of 685 samples) (Parsons *et al*. 2007). The fragments represented a diversity of bryophytes (15 families of mosses, thallose and leafy liverworts) and ranged from whole plants to detached leaves. The bryophytes evidenced effects of being eaten: highly fragmented, abraded, tightly interwoven with hair and fiber content. The bryophytes mixed with hair suggested that they may have been ingested during grooming.

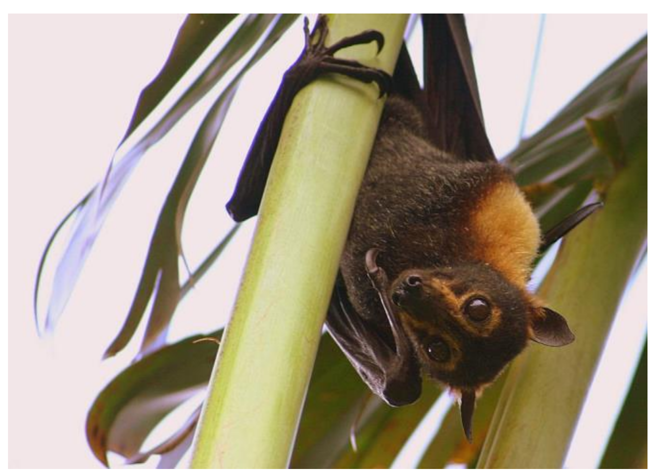

Figure 58. ***Pteropus conspicillatus***, the spectacled flying fox, with folded wings. This bat is a moss disperser. Photo by Shek Graham, through Wikimedia Commons.

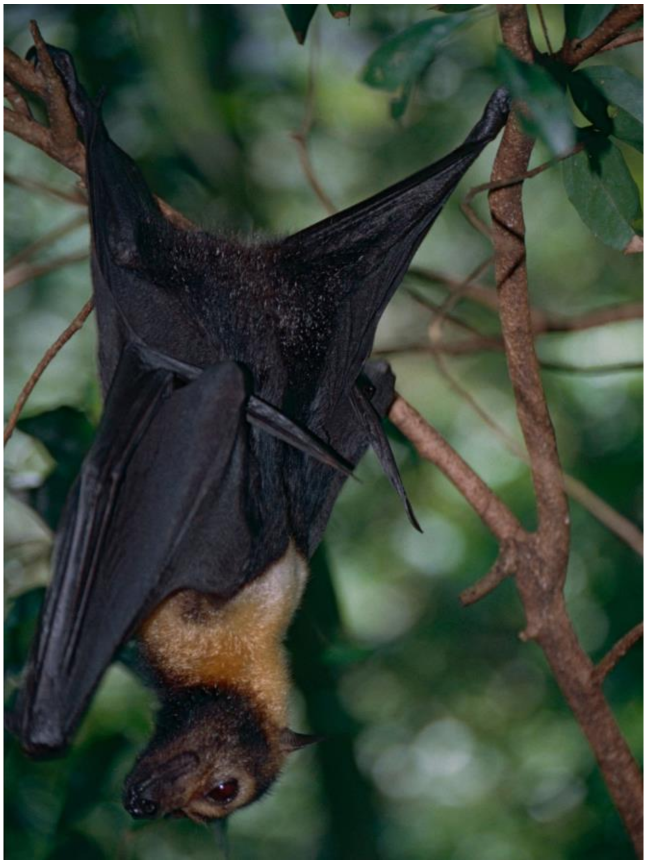

Figure 59. ***Pteropus conspicillatus*** showing the bat wings. Photo by Bernard Dupont, through Creative Commons.

The use of bryophytes as food may be accidental or at least of only minor significance. On the other hand, the flying fox appears to be an effective dispersal vector. Using material from the interior of the feces (Figure 60-Figure 61), Parsons (Figure 60) and coworkers (2007) demonstrated that 52% of 48 fragments developed rhizoids and/or shoots in culture. Seasonal effects were evident, with those collected early in the season having greater germination success (17 of 28 fragments) than those collected later in the growing season (7 of 20).

Figure 60. ***Jennifer Parsons*** and splat trap for ***Pteropus conspicillatus***. Photo courtesy of Andi Cairns.

Figure 61. ***Pteropus conspicillatus*** splat on a leaf. Photo courtesy of Andi Cairns.

Summary

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

The Merriam chipmunk gathers mosses, presumably for nesting material, but it could possibly be for food. The Eurasian red squirrel uses mosses in its nest, possibly to buffer the temperature, and possibly also explaining use by the Arctic ground squirrels in their hibernacula. Flying squirrels include mosses in the nest, presumably for the same purpose. The grey squirrel includes mosses to line the nest. The red squirrel uses mosses to decorate its home. Pikas use the mosses as a cool cover during hot days. Pleurocarpous mosses are often preferred for nesting.

Uses for food are less common among these larger rodents, but the Arctic ground squirrels cache moss capsules for winter food. The Arctic hare likewise consumes moss capsules. The European rabbit eats the leafy portions, but it is choosey about which species it eats. Pikas eat mosses when they are abundant. They re-ingest their feces, permitting them to obtain more

nutrients from ingested mosses. Even the flying fox (actually a bat) ingests mosses, and in the process it serves as a dispersal agent.

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

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, an Isle Royale researcher, provided me with the tentative identification of a juvenile ***Peromyscus*** based on the picture alone. Andi Cairns alerted me to the study on the spectacled flying fox. Johanna Varner helped me get images of pikas. Thank you to Brent Mishler for helping me to get all the information I needed regarding the CAMcorder observations of the Merriam chipmunk and to Des Callaghan for helping me retell the story of the role of rabbits in making a habitat for ***Scopelophila cateractae***.

Literature Cited

Barnes, B. M. 1989. Freeze avoidance in a mammal: Body temperatures below 0°C in an Arctic hibernator. Science 244: 1593-1595.

Barrio, I. C., Hik, D. S., Peck, K., and Bueno, C. G. 2013. After the frass: Foraging pikas select patches previously grazed by caterpillars. Biol. Lett. 9: 20130090; DOI: 10.1098/rsbl.2013.0090.

Beever, E. A., Ray, C., Mote, P. W., and Wilkening, J. L. 2010. Testing alternative models of climate-mediated extirpations. Ecol. Appl. 20: 164-178.

Beever, E. A., Ray, C., Wilkening, J. L., Brussard, P. F., and Mote, P. W. 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biol. 17: 2054-2070.

Bhadresa, R. 1977. Food preferences of rabbits *Oryctolagus cuniculus* L. at Holkham Sand Dunes, Norfolk. J. Appl. Ecol. 14: 287-291.

Callaghan, Des. 2015. Rare copper-moss befriends rabbits. Accessed 16 February 2015 at <http://www.bryophytesurveys.co.uk/rare-copper-moss-befriends-rabbits/>.

Ciechanowski, M., Cichocki, J., Ważna, A., and Piłacińska, B. 2012. Small-mammal assemblages inhabiting *Sphagnum* peat bogs in various regions of Poland. Biol. Lett. 49(2): 115-133.

Clément, B. and Touffet, J. 1981. Vegetation dynamics in Brittany heathlands after fire. Vegetatio 46: 157-166.

Clough, G. C. and Albright, J. J. 1987. Occurrence of the northern bog lemming, *Synaptomys borealis*, in the northeastern United States. Can. Field-Nat. 101: 611-613.

Conner, D. A. 1983. Seasonal changes in activity patterns and the adaptive value of haying in pikas (*Ochotona princeps*). Can. J. Zool. 61: 411-416.

Davidson, A. J., Harborne, J. B., and Longton, R. E. 1990. The acceptability of mosses as food for generalist herbivores, slugs in the Arionidae. Bot. J. Linn. Soc. 104: 99-113.

Dearing, M. D. 1996. Disparate determinants of summer and winter diet selection of a generalist herbivore, *Ochotona princeps*. Oecologia 108: 467-478.

Dearing, M. D. 1997a. The function of haypiles of pikas (*Ochotona princeps*). J. Mammal. 78: 1156-1163.

Dearing, M. D. 1997b. The manipulation of plant toxins by a food-hoarding herbivore, *Ochotona princeps*. Ecology 78: 774-781.

Defenders of Wildlife. 2017. Climate change and the pika. Accessed 30 December 2017 at <https://defenders.org/sites/default/files/publications/carbon_dioxide_and_the_pika.pdf>.

Gillham, M. E. 1954. An annotated list of the bryophytes and lichens of Skokholm Island, Pembroke shire. Northw. Nat. 1954: 37-48.

Gillham, M. E. 1955. Ecology of the Pembrokeshire Islands III. The effect of grazing on the vegetation. J. Ecol. 43: 172-206.

Gillis, E. A., Morrison, S. F., Zazula, G. D., and Hik, D. S. 2005. Evidence for selective caching by Arctic ground squirrels living in alpine meadows in the Yukon. Arctic 58: 354-360.

Goheen, J. R. and Swihart, R. K. 2003. Food-hoarding behavior of gray squirrels and North American red squirrels in the central hardwoods region: Implications for forest regeneration. Can. J. Zool. 81: 1636-1639.

Graham, E. A., Hamilton, M. P., Mishler, B. D., Rundel, P. W., and Hansen, M. H. 2006. Use of a networked digital camera to estimate net CO_2 uptake of a desiccation-tolerant moss. Internat. J. Plant Sci. 167: 751-758.

Greene, R. G. (ed.). 1887. The International Cyclopedia: A Compendium of Human Knowledge, Volume 13. Dodd, Mead & Co., New York, p. 751.

Groves, C. and Yensen, E. 1989. Rediscovery of the northern bog lemming (*Synaptomys borealis*) in Idaho. Northw. Nat. 70: 14-15.

Hamilton, W. J. Jr. 1941. On the occurrence of *Synaptomys cooperi* in forested regions. J. Mammal. 22: 195-195.

Hanrahan, Christine. 2012. Red squirrels (*Tamiasciurus hudsonicus*) at the FWG. Accessed 1 January 2018 at <http://www.ofnc.ca/fletcher/flora-fauna/squirrels/red-squirrels_e.php>.

Harvey, T. and Polite, C. 1999. California Wildlife Habitat Relationship System. Accessed 7 May 2004 at <http://www.dfg.ca.gov/whdab/html/M060.html>.

Horsfall, R. 1925. The pika at sea level. J. Mammal. 6: 201-202.

Huntly, N. J., Smith, A. T., and Ivins, B. L. 1986. Foraging behavior of the pika (*Ochotona princeps*), with comparisons of grazing versus haying. J. Mammal. 67: 139-148.

IUCN. 2017. *Glaucomys sabrinus* (Carolina Flying Squirrel, Northern Flying Squirrel). Accessed 1 January 2018 at <http://www.iucnredlist.org/details/39553/0>.

Koju, N. P. and Chalise, M. K. 2015. Food hoarding behaviour of pika (*Ochotona*) in Langtang National Park, Nepal. J. Nat. Hist. Mus. 28: 34-41.

Laar, V. van. and Dirkse, G. M. 2010. Bladmossen en kortmossen als nestmateriaal van kleine zoogdiersoorten. Buxbaumiella 85: 36-41.

MacArthur, R. A. and Wang, L. C. H. 1973. Physiology of thermoregulation in the pika, *Ochotona princeps*. Can. J. Zool. 51: 11-16.

MacArthur, R. A. and Wang, L. C. H. 1974. Behavioral thermoregulation in the pika, *Ochotona princeps*: A field study using radiotelemetry. Can. J. Zool. 52: 353-358.

Marchand, P. J. 2001. A squirrel's glide to a long life. Nat. Hist. 110(8): 18-19.

Mishler, B. D. and Hamilton, M. P. 2002. The MossCam project: The world's first remote sensing project on moss ecology. American Bryological and Lichenology Society Abstracts of Contributed Papers 2002: 32.

Morrison, S., Barton, L., Caputa, P., and Hik, D. S. 2004. Forage selection by collared pikas, *Ochotona collaris*, under varying degrees of predation risk. Can. J. Zool. 82: 533-540.

Morrison, S. F., Pelchat, G., Donahue, A., and Hik, D. S. 2009. Influence of food hoarding behavior on the over-winter survival of pikas in strongly seasonal environments. Oecologia 159: 107-116.

Parsons, J. G., Cairns, A., Johnson, C. N., Robson, S. K. A., Shilton, L. A., and Westcott, D. A. 2007. Bryophyte dispersal by flying foxes: A novel discovery. Oecologia 152: 112-114.

Patterson, J. E., Patterson, S. J., and Malcolm, R. J. 2007. Cavity nest materials of northern flying squirrels, *Glaucomys sabrinus*, and North American red squirrels, *Tamiasciurus hudsonicus*, in a secondary hardwood forest of southern Ontario. Can. Field-Nat. 121: 303-307.

Pearson, D. E. 1991. The Northern Bog Lemming in Montana and the Contiguous United States: Distribution, Ecology and Relic Species Theory. Unpubl. Senior Thesis, Univ. Mont., Missoula, 33 pp.

Pulliainen, E. and Raatikainen, M. 1996. Insulative properties of some drey materials of the red squirrel, *Sciurus vulgaris* L. Aquilo, Series Zoologica 29: 43-47.

Quinton, M. S. 1997. Seasons of the boreal forest. Biol. Digest 24(4): 10-17.

Ranwell, D. S. 1960. Newborough Warren, Anglesey: III. Changes in the vegetation on parts of the dune system after the loss of rabbits by myxomatosis. J. Ecol. 48: 385-395.

Richardson, D. 1981. The Biology of Mosses. Halsted Press, New York, 290 pp.

Reichel, J. D. and Beckstrom, S. G. 1993. Northern bog lemming survey: 1992. [Unpublished report] Montana Natural Heritage Program, Helena, MT, 64 pp.

Simpson, W. G. 2009. American pikas inhabit low-elevation sites outside the species' previously described bioclimatic envelope. W. N. Amer. Nat. 69: 243-250.

Smith, A. T. 1974. The distribution and dispersal of pikas: Influences of behavior and climate. Ecology 55: 1368-1376.

Smith, A. T. and Boyer, A. F. 2008. *Oryctolagus cuniculus*. The IUCN Red List of Threatened Species 2008: e.T41291A10415170. Accessed 1 January 2018 at <http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T41291A10415170.en>.

Steele, M. A., Hadj-Chikh, L. Z., and Hazeltine, J. 1996. Caching and feeding decisions by *Sciurus carolinensis*: Responses to Weevil-infested acorns. J. Mammal. 77: 305-314.

TalkTalk: Nest. 2011. Accessed 29 October 2011 at <http://www.talktalk.co.uk/reference/encyclopaedia/hutchinson/m0063746.html>.

Tripp, F. E. 1888. British mosses, their homes, aspects, structure and uses. George Bell & Sons, Covent Garden, London (Wheldon & Wesley), 2 Vols.

Varner, J. and Dearing, M. D. 2014a. Dietary plasticity in pikas as a strategy for atypical resource landscapes. J. Mammal. 95: 72-81.

Varner, J. and Dearing, M. D. 2014b. The importance of biologically relevant microclimates in habitat suitability assessments. PLoS One 9(8): e104648.

Watt, A. S. 1957. The effect of excluding rabbits from Grassland B (*Mesobrometum*) in Breckland. J. Ecol. 45: 861-878.

Whitaker, J. O. Jr. 2004. *Sorex cinereus*. Mammal. Spec. 743: 1-9.

Wikipedia. 2017a. Erinaceidae. Last updated 7 October 2017. Accessed 17 November 2017 at <https://en.wikipedia.org/wiki/Erinaceidae>.

Wildscreen. 2010. *Erinaceus europaeus*. EOL. Accessed 17 November 2017 at <http://eol.org/pages/1178684/overview>

Youngman, P. M. 1975. Mammals of the Yukon Territory. National Museums of Canada. Publ. Zool. 10: 1-192.

YPTE. 2011. Grey squirrel: *Sciurus carolinensis*. Accessed 29 October 2011 at <http://www.ypte.org.uk/animal/squirrel-grey-/176>.

Zazula, G. D., Froese, D. G., Elias, S. A., Kuzmina, S., La Farge, C., Reyes, A. V., Sanborn, P. T., Schweger, C. E., Smith, C. A. S., and Matthews, R. W. 2006. Vegetation buried under Dawson tephra (25,300 14C yr BP) and locally diverse late Pleistocene paleoenvironments of Goldbottom Creek, Yukon, Canada. Palaeogeogr. Palaeoclimatol. Palaeobiol. 242: 253-286.