CHAPTER 16-2
BIRDS AND BRYOPHYTIC FOOD SOURCES

TABLE OF CONTENTS

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Figure 1. ***Branta bernicla hrota***, Brant, juvenile foraging; foods include bryophytes. Photo by MPF, through Creative Commons.

Many birds do depend on bryophytes for food. Some eat the leafy gametophytes, especially in the Arctic. Others use the more nutrient-rich capsules. And others, probably many more than we know, forage for macroinvertebrates among the bryophytes, especially epiphytes.

Capsules

A. J. Grout, one of the earliest of North American bryologists, observed birds pecking the capsules of ***Polytrichum commune*** (Figure 2), a story retold by Lewis Anderson (Bryonet 10 April 2003). To this story, Frank Cook (Bryonet 15 May 2001) contributed his own observations of White-throated Sparrows (***Zonotrichia albicollis***; Figure 3) "vigorously nipping the capsules from ***Polytrichum*** in a white pine (***Pinus strobus***; Figure 4) stand in Algonquin Park, Ontario.

Figure 2. ***Polytrichum commune*** capsules, food for White-throated Sparrows (***Zonotrichia albicollis***) and Norwegian Grouse (***Tetrao urogallus***?) chicks. Photo by Bob Klips, with permission.

Figure 3. ***Zonotrichia albicollis***, White-throated Sparrow, a consumer of ***Polytrichum*** capsules. Photo by Dorothy Pugh, with permission.

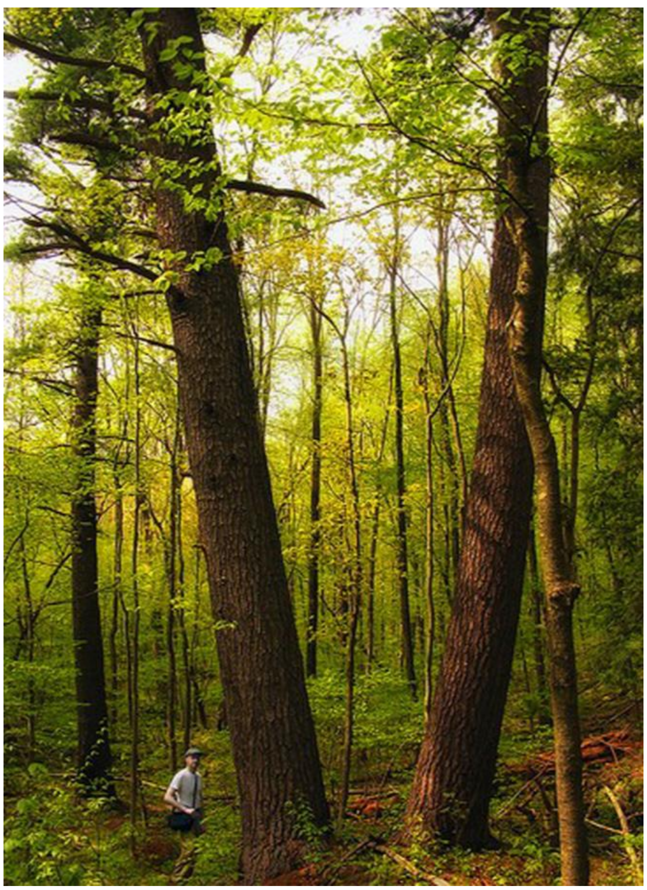

Figure 4. ***Pinus strobus*** (white pine) forest, Pennsylvania. Photo by Nicholas T., through Creative Commons.

Richardson (1981) reported moss-feeding by mammals and birds in northern areas. Capsules of ***Bryum*** (Figure 5) and ***Polytrichum*** (Figure 2) are eaten by the Norwegian Grouse chicks (***Tetrao urogallus***?; Figure 6), apparently as the main food, whereas other kinds of capsules are eaten by Scottish Red Grouse (***Lagopus lagopus scotica***; Figure 7) (Lid & Meidell 1933). The Wyoming Sage Grouse (***Centrocercus urophasianus***; Figure 8) eats small amounts of moss, Snow Buntings (***Plectrophenax nivalis***; Figure 9) eat ***Bryum algovicum*** capsules (Figure 10), and the Moorhen (***Gallinula chloropus***; Figure 11), Blackbird (***Turdus merula***; Figure 12), Song Thrush (***Turdus philomelos***; Figure 13), and Fieldfare (***Turdus pilaris***; Figure 14) all eat mosses. In Britain, the Blue Tits (***Cyanistes caeruleus***; Figure 15) and Marsh Tits (***Poecile palustris***; Figure 16) feed on capsules of ***Dicranoweisia cirrata*** (Figure 17) (Betts 1955). Catherine La Farge reported on Bryonet (15 January 2008) that high Arctic moss capsules are consumed by lemmings and Arctic hares. Thus it would not be surprising if birds also consume them when the capsules are still green.

Figure 5. ***Bryum arcticum*** with capsules that serve as food for Norwegian Grouse (***Tetrao urogallus***?) chicks in Norway. Photo by Michael Lüth, with permission.

Figure 6. ***Tetrao urogallus***, Norwegian Grouse female, on moss. Chicks of this species eat capsules of ***Bryum*** and ***Polytrichum***. Photo by Honza Sterba, through Creative Commons.

Figure 7. ***Lagopus lagopus scotica***, Red Grouse, a species that eats moss capsules. Photo by MPF, through Creative Commons.

Figure 8. ***Centrocercus urophasianus***, Greater Sage Grouse, a consumer of small amounts of mosses. Photo by Gordon Sherman, with online permission.

Figure 9. ***Plectrophenax nivalis***, Snow Bunting, a herbivore on the capsules of ***Bryum pendulum***. Photo by Cephas, through Creative Commons.

Figure 10. ***Bryum algovicum*** with capsules that are eaten by the Snow Bunting. Photo by Barry Stewart, with permission.

Figure 11. ***Gallinula chloropus***, Moorhen, a moss consumer. Photo from Anemone Projectors, through Creative Commons.

Figure 12. ***Turdus merula***, a Blackbird that eats mosses. Photo by Mario Modesto Mata through GNU Free Documentation.

Figure 13. ***Turdus philomelos***, Song Thrush, in Cambridgeshire, a bird that eats mosses. Photo by Brian Eversham, with permission.

Figure 14. ***Turdus pilaris***, Fieldfare, a bird that eats mosses. Photo by Frankie Fouganthin, through Creative Commons.

Figure 15. ***Cyanistes caeruleus***, Blue Tit, in winter, a bird that eats capsules of ***Dicranoweisia cirrata***. Photo through public domain.

Figure 16. ***Poecile palustris***, Marsh Tit, a species that eats capsules of ***Dicranoweisia cirrata***. Photo by Luc Viatour, through Creative Commons.

Figure 17. ***Dicranoweisia cirrata*** with capsules that are eaten by Blue Tits and Marsh Tits. Photo from BioPix, through Creative Commons.

Dan Norris (Bryonet, 22 November 1995 & 19 November 2006) reported that the Green Eastern Rosella Parrot (***Platycercus eximius***; Figure 18) in Tasmania selects the green, but mature, capsules of ***Polytrichum juniperinum*** (Figure 19) on clay soil banks as a primary food source. He watched the parrots for over an hour, then examined the area to find that they clipped the setae at 45º angles and left a miniature forest of setae with a litter of calyptrae that were split off, falling 5-10 mm to the right of the sporophyte. The number of barren setae suggested that harvest in this manner was widespread. Further examination on other clay banks of the island revealed that similar patterns were common in the forested mid-elevation habitats throughout the island.

Ptarmigans

In northern Europe and Alaska, the Willow Ptarmigan (***Lagopus lagopus***; Figure 20-Figure 21, Figure 23) chicks consume moss capsules of ***Polytrichum*** *s.l.* (Figure 19) and ***Pohlia*** (Figure 22) (Weeden 1969; Gardarsson & Moss

1970; Spidsø 1980; Martin & Hik 1992). Pullianen and Eskonen (1982) considered that moss capsules could be a source of high quality food in this Arctic environmental at a time when they were too small to handle large food items.

Figure 18, ***Platycercus eximius diemenensis***, Green Eastern Rosella Parrot male, a species that selects green capsules of ***Polytrichum juniperum*** as food. Photo by J. J. Harrison, through Creative Commons.

Figure 19. ***Polytrichum juniperinum*** mature capsules that are still green under the calyptra, providing food for the Green Eastern Rosella Parrot (***Platycercus eximius***). Photo by Ian Sutton, through Creative Commons.

Figure 20. ***Lagopus lagopus lagopus***, Willow Ptarmigan in summer plumage. Chicks of this species consume mosses. Photo by George Lesard, through Creative Commons.

The consumption of these moss capsules by Willow Ptarmigan chicks appears to be a regular event every spring as the capsules appeared in the diet in three consecutive years (Martin & Hik 1992). It is likely that they supply needed lipids; they contain about 20% lipids, a level higher than that in the other available vegetation (Pakarinen & Vitt 1974). In two cases the large numbers of capsules consumed suggest food selection rather than accidental ingestion (Martin & Hik 1992).

Figure 21. ***Lagopus lagopus lagopus***, Willow Ptarmigan in winter plumage. Chicks of this species eat capsules of ***Polytrichum*** and ***Pohlia***. Photo through Creative Commons.

Figure 22. ***Pohlia nutans*** with capsules. Capsules from this genus are eaten by the Willow Ptarmigan in the North. Photo by Michael Lüth, with permission.

Martin and Hik (1992) found the crops of Willow Ptarmigan chicks (***Lagopus lagopus***; Figure 23) stuffed with capsules of the moss ***Distichium inclinatum*** (Figure 24). The researchers suggested that the sporophytes might be easily accessible forage for these chicks. Could the capsules possibly act as grinding agents for other foods?

Figure 23. ***Lagopus lagopus lagopus*** *cf* ***pullus***, Willow Ptarmigan juvenile, a consumer of moss capsules of ***Polytrichum*** and ***Pohlia***. Photo by Walter Pfliegler, with permission.

Figure 24. ***Distichium inclinatum*** with capsules. Willow Ptarmigan chicks eat the capsules and they can be found in the crops of the birds. Photo by Michael Lüth, with permission.

Grouse

Grouse (**Tetraoninae**) chicks (Figure 7) are known to eat moss capsules (Richardson 1981). In fact, the clutch size and mean egg weight are dependent on the food of the mother (Naylor & Bendell (1989). The two most preferred foods were the trailing arbutus (*Epigaea repens*; Figure 25) and capsules of ***Polytrichum*** (Figure 19), and their availability was important, but not the size of the hen or her scaled body weight. Egg size, on the other hand, was not related to spring diet, but was instead related to the size of the hen. Therefore, the spring diet was important in providing the nutrients required for clutch formation.

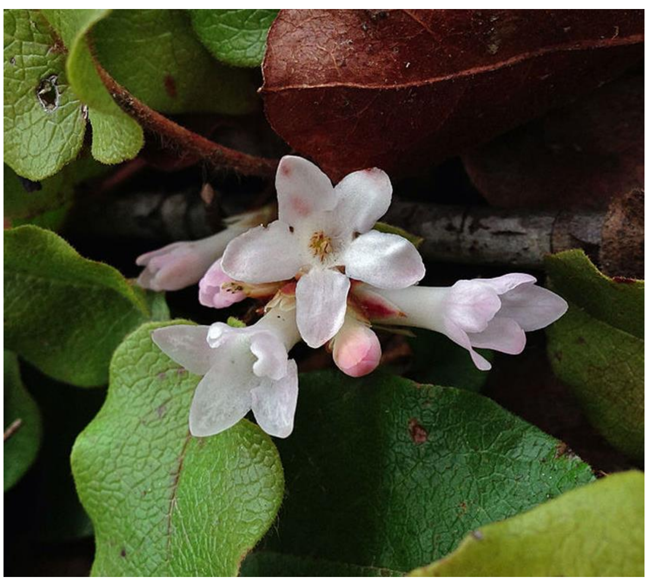

Figure 25. ***Epigaea repens***, one of the two most preferred foods of grouse chicks. Photo by Fritz Flohr Reynolds, through Creative Commons.

Titmice

Titmice eat moss capsules in the temperate zone (Richardson 1981). Haftorn (1954) on five occasions observed the Crested Titmouse (***Baeolophus*** sp.; Figure 26) on snow-free rocks with mosses. The birds were pulling at the tips of the moss and Haftorn surmised that they were probably eating the capsules.

Figure 26. ***Baeolophus***, Crested Titmouse, a genus that grazes on the tips of mosses, perhaps to eat capsules. Photo by Dick Daniels, through Creative Commons.

Betts (1955) considered that in oak woodlands the Great Tit (***Parus major***; Figure 27) and the Blue Bit (***Cyanistes caeruleus***; Figure 15) can compete for food with the Coal Tit (***Periparus ater***; Figure 28) and the Marsh Tit (***Poecile palustris***; Figure 29). Using gizzard analyses, she determined that the Great Tit and Blue Tit had different diets, with the former feeding mostly on adult insects, especially weevils, and the Blue Tit on scale insects, small larvae, and pupae. The Coal Tit fed mostly on small, free-living insects and scales. The Marsh Tit ate mostly adult insects, scales, and a few larval forms. But in winter the diet changed. The Blue Tit consumed large numbers of capsules from the moss ***Dicranoweisia cirrata*** (Figure 30), ignoring the capsules of all other species. It had so many capsules in its gizzard that the gizzard was a vivid green (300-450 capsules per gizzard). One Coal Tit had consumed a few capsules and one Marsh Tit had 233 capsules in the gizzard.

Figure 27. ***Parus major***, Great Tit, a consumer of adult insects. Photo by Francis Franklin, through Creative Commons.

Figure 28. ***Periparus ater***, Coal Tit, a species that feeds on small, free-living insects and scales, but consumes large numbers of moss capsules in winter. Photo by David Kesl, through Creative Commons.

Figure 29. ***Poecile palustris***, Marsh Tit, a species that switches to eating moss capsules in the winter. Photo by Luc Viatour, through Creative Commons.

Figure 30. ***Dicranoweisia cirrata*** with capsules that provide winter food for the Blue Tit (***Cyanistes caeruleus***; Figure 15). Photo from BioPix, through Creative Commons.

In Norway, one might see the Crested Tit (***Parus cristatus***; Figure 31) pulling on moss tips that are free from snow on rocks in December (Haftorn 1954).

Figure 31. ***Parus cristatus***, Crested Titmouse, a species that harvests mosses in early winter. Photo by Jiří Duchoň, through Creative Commons.

Kōkako

The Kōkako/Blue-wattled Crow (***Callaeas wilsoni***; Figure 32) in New Zealand feeds on moss capsules (Jessica Beever, Bryonet 2 May 2003, based on observations by personnel from the Department of Conservation). Of 912 observations, 26 were feeding on moss capsules. When it was a good year for tracheophytes, only 3 out of 217 observations were of capsule feeding, but in a poor-fruit year, this increased to 6 out of 178 on mosses. These are probably within normal variation, but it suggests that the moss capsules may serve as an emergency food. The Kōkako forage along the branches, snipping off the capsules with the edge of the beak. Although they also feed on invertebrates from the bark and mosses, their action in obtaining the mosses by deliberate cutting is different from the pecking used to obtain insects. Eating the capsules is no accident.

The Kōkako (***Callaeas wilsoni***) make their greatest use of mosses in spring and summer (3%) when the capsules are most abundant, but they also may consume some in winter (0.75%) (Jessica Beever, Bryonet 2 May 2003, based on observations by personnel from the Department of Conservation). The actual consumption may be larger as it is more difficult to observe moss feeding than that on bright-colored fruits.

Figure 32. ***Callaeas wilsoni***, Kōkako, a bird that feeds on moss capsules. Photo by Duncan, through Creative Commons.

Fruit Mimicry by Capsules?

Michael Lüth (Bryonet 16 January 2008) has observed that some members of the **Splachnaceae** change their odor as they mature. ***Tetraplodon mnioides*** (Figure 33) has violet-colored capsules that smell like blueberries when the capsules are still closed. Once the capsules open, the odor changes to the smell of dung. A similar change occurs in ***Splachnum ampullaceum*** (Figure 34). When this species has immature capsules, the capsules have a strong, sweet odor like berries. But once the capsule opens it smells like dung. Could it be that in these early fruity stages the capsules are eaten by the local fauna, including birds? Patricia Geissler once expressed the idea that birds eat the capsules of ***Voitia nivalis*** (Figure 35) that occur among the buds of *Salix herbacea* (Figure 36), an early season food for some of the Arctic birds. If so, this is another potential dispersal mechanism. One might be able to make some interesting observations from within a duck blind, or using time-lapse photography.

Figure 33. ***Tetraplodon mnioides*** with mature capsules that might be eaten by the local fauna. Photo by Richard Caners, with permission.

Figure 34. ***Splachnum ampullaceum***, showing capsules that resemble some of the nearby fruits. Photo by Michael Lüth, with permission.

Figure 35. ***Voitia nivalis*** with capsules on Svalbard. These capsules resemble fruits of *Salix herbacea* (Figure 36) and may be eaten along with them. Photo by Michael Lüth, with permission.

Figure 36. *Salix herbacea* fruits in Austria, resembling capsules of ***Voitia nivalis***. Photo by El Grafo, through Creative Commons.

While in Tasmania in December for the Australasian Bryological Workshop, Paddy Dalton and Rod Seppelt showed their fellow bryologists ***Pleurophascum grandiglobum*** (Figure 37), a moss of the button grass plains in SW Tasmania. Allison Downing (Bryonet 18 January 2008) was "intrigued by the capsules (Figure 37), which are extremely large, globular, cleistocarpous, and on quite long setae, and was curious about dispersal, particularly the possibility that this species might be dispersed by birds. The capsules are light green, fading to pale yellow, and to me, had much in common with the fruits of many Epacridaceae (Ericaceae) and also of *Persoonia* (Proteaceae; Figure 38) that grow in this area." Emma Pharo stated that there are a number of birds that do feed on the ground in the button grass plains (Allison Downing, Bryonet 18 January 2008). The birds might not gain any nutrition from the capsules and their contents, but mimicry is used by many plants for pollination so why not for dispersal? The New Zealand species of ***Pleurophascum***, similarly, has globular fruits that become orange/red with maturity, and the color (red, orange) would make them even more attractive to birds.

Figure 37. ***Pleurophascum grandiglobum*** with capsules that are large and may be eaten by birds and dispersed by them. Photo by Christopher Taylor, Australian National Botanic Gardens, with online permission.

Figure 38. *Persoonia levis* fruit; ***Pleurophascum grandiglobum*** capsules (Figure 37) mimic these and may be eaten by some of the same bird species. Photo by John Tann, through Creative Commons.

Michael Lüth's comment about ***Tayloria*** (Figure 39-Figure 41) reminded Downing that three species of ***Tayloria***, ***T. octoblepharum*** (Figure 39), ***T. gunnii*** (Figure 40), and ***Tayloria tasmanica*** (Figure 41), all with abundant and conspicuous capsules, grow in the same habitat as ***Pleurophascum*** (Figure 37). Perhaps they, too, are fragrant (like the fruits of some Ericaceae) in their early stages of development and dispersed by birds before they reach the 'dung'-smelling stage of their life cycle.

Figure 39. ***Tayloria octoblepharum*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Janice Glime.

Figure 40. ***Tayloria gunnii*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Christopher Taylor, Australian National Botanic Gardens, with online permission.

Figure 41. ***Tayloria tasmanica*** with capsules, possible mimics of some of the fruits in the Ericaceae. Photo by Paddy Dalton, with permission.

Bird Color Vision

To understand bird choice based on color, it is necessary to understand how birds see color. Most studies on bird responses to color have assumed that they see colors the same way as humans do (Bennett *et al*. 1994). However, this is not true. The human eye design is different from that of birds and has different spectral abilities. Birds have four types of cones in the retina, compared to our three (Finger & Burkhardt 1994). Among their differences, at least some birds are able to see UV light, and feathers of some birds reflect UV light (Bennett & Cuthill 1994).

Using gene coding for UV- or violet-absorbing opsin in the retina, Ödeen & Håstad (2003) were able to assess color sensitivities on living birds. Their color vision can be put into two classes: short-wavelength sensitivity biased toward violet and another biased toward UV. The violet sensitivity is ancient among birds, and sensitivity to UV has evolved independently in four evolutionary lines. Many members of the orders **Psittaciformes** (parrots) and **Passeriformes** (perching birds) present UV-sensitive type color vision, but within the **Passeriformes**, the **Corvidae** (Jays, Magpies, & Crows) and **Tyrannidae** (Tyrant Flycatchers) do not. At least some members of **Laridae** (Skuas, Gulls, Terns, & Skimmers – **Charadriiformes**) and **Struthionidae** (flightless birds – **Struthioniformes**) likewise have UV-sensitive vision. Birds of prey (**Accipitridae** & **Falconidae** – **Falconiformes**), on the other hand, have the violet type.

The colorations of songbirds are significantly more conspicuous to other songbirds than they are to raptors and covids in the coniferous and deciduous forests (Finger & Burkhardt 1994; Håstad *et al*. 2005). This difference permits the **Passeriformes** to advertise their colors for mating purposes while not advertising to the raptors (birds of prey) that are their predators.

In addition to their cones birds have a complex of oil droplets in their retinas that may alter the color hues they perceive and that may also alter brightness and saturation (Bennett *et al*. 1994). Bennett and coworkers caution us that color is a product of the perception of the observer.

This brings us to the question of bird choice of bryophyte capsules and leafy stalks based on color. We know that bryophytes often serve as emergency food. Consider the observation of Bennett and Théry (2007) that plants are most likely to produce conspicuous fruit colors at times when frugivorous bird abundance is low. By contrast, if seeds, or bryophyte spores, are dispersed by birds, then I would think it would be beneficial for the fruits and capsules if they were bright-colored when it is appropriate for dispersal.

But capsules are not the only parts of bryophytes that are eaten. As you will soon see, leafy parts are as well. And we know that at least some bryophytes have fluorescent cell walls. For example, the bulbils of ***Pohlia*** are fluorescent under UV light (Nordhorn-Richter 1984). The value of this fluorescence for dispersal by birds remains unexplored.

Leafy Plants

It is uncommon for birds to use leafy bryophytes for food, but they may do so when food is scarce (Sillett 1994; Rhoades 1995; Wolf 2009). Among the few birds that actually eat the leafy bryophytes, we know that the Red-throated Loon (***Gavia stellata***; Figure 42), Brant (***Branta bernicla***; Figure 1), White-tailed Ptarmigan (***Lagopus leucura***; Figure 43), Willow Ptarmigan (***Lagopus lagopus lagopus***; Figure 44), and Rock Ptarmigans (***Lagopus muta***; Figure 45) all eat bryophytes in the Pacific Northwest, USA (Palmer 1962; Martin & Hik 1992; Braun *et al*. 1993; Hannon *et al*. 1998).

Figure 42. The Red-throated Loon, ***Gavia stellata***, and young. This species actually eats the leafy bryophytes in the Pacific Northwest, USA. Photo by David Karnå, through Creative Commons.

Figure 43. ***Lagopus leucura***, White-tailed Ptarmigan, Rocky Mountains, Alberta, a species that eats leafy bryophytes in the Arctic. Photo by John Hill, through Creative Commons.

Figure 44. ***Lagopus lagopus lagopus***, Willow Ptarmigan, with summer plumage, sitting on its dinner plate of leafy bryophytes. Photo by George Lesard, through Creative Commons.

Figure 45. ***Lagopus muta***, Rock Ptarmigan in summer plumage, a species that eats leafy bryophytes. Photo by Böhringer Friedrich, through Creative Commons.

Ducks and Food Availability

For ducks, bryophytes are not a preferred food. Ring-necked Ducks (***Aythya collaris***; Figure 46) in temporary wetlands use mostly plants, but those in more permanent wetlands choose animal foods for half their diet. The period during pre-laying and laying is an important time for females to obtain protein, and in the northern long days of Minnesota, USA, the females may feed up to 19 hours a day to obtain needed protein. However, when their usual food sources are unavailable, Ring-necked Ducks (***Aythya collaris***) may eat bryophytes (Hohman 1985). In 1980, reduced protein content in Class II juveniles seemed to be the result of a large percentage of aquatic mosses and caddisflies in cases. In that year, aquatic mosses comprised 18% of the diet, whereas in other years there were only trace amounts.

Figure 46. ***Aythya collaris***, Ring-necked Duck male, a species that obtains protein from mosses. Photo by Alan Vernon, through Creative Commons.

Geese

Geese seem to have a love-hate relationship with mosses as a food source. Sometimes they are essential to the diet, but in other times and places, they are deliberately avoided. The Canada Goose (***Branta canadensis***; Figure 47) selectively consumes the riverweed *Podostemum ceratophyllum* (Figure 48) over the moss ***Fontinalis novae-angliae*** (Figure 49) in a riverine system, despite the dominance (89% of biomass) of moss in that system. This preference may have been due to the presence of C18 acetylenic acid, octadeca-9,12-dien-6-ynoic acid in the mosses, a compound that deters crayfish feeding.

Figure 47. ***Branta canadensis***, Canada Geese and goslings. This species avoids eating the moss ***Fontinalis***. Photo by Janice Glime.

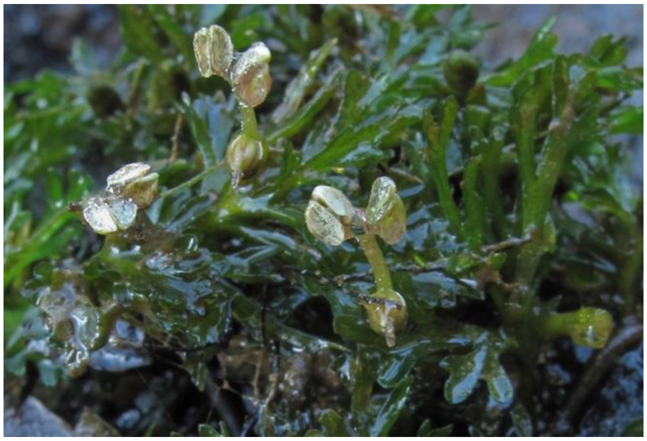

Figure 48. *Podostemum ceratophyllum*, a flowering plant species that is preferred over mosses as food by Canada Geese. Photo by Alan Cressler, with permission.

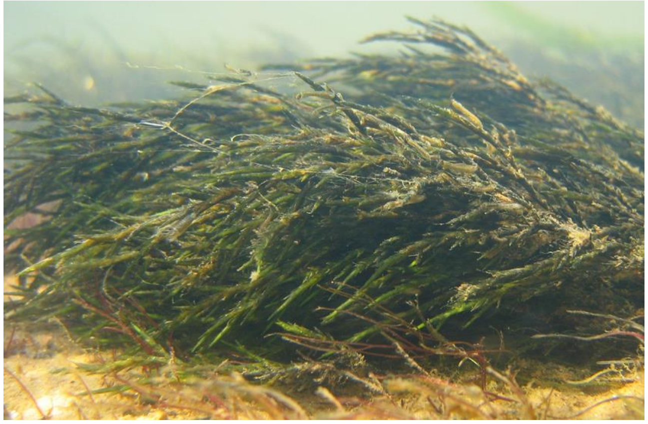

Figure 49. ***Fontinalis novae-angliae*** protecting invertebrates from Canada Goose grazing because the geese won't eat it. Photo by John Parker, with permission.

By contrast, polar and alpine habitats seem to encourage the consumption of bryophytes, including by geese (Longton 1992). Gloutney *et al*. (2001) report that at Karrak Lake, NT, Canada Geese (***Branta canadensis***; (Figure 47), Lesser Snow Geese (***Chen caerulescens caerulescens***; Figure 50) and Ross's Geese (***Chen rossii***; Figure 51) eat primarily mosses, chickweed (*Stellaria* spp.; Figure 52), and sedges (*Carex* spp.; Figure 53). In the Svalbard breeding season, mosses form a considerable part of the diet of Barnacle Geese (***Branta leucopsis***; Figure 54) (Prop *et al*. 1980).

Figure 50. ***Chen caerulescens***, Lesser Snow Geese, grazing on sedges. Photo by Walter Siegmund, through Creative Commons.

Figure 51. ***Chen rossii***, Ross's Goose, grazing on sedges. Photo by Andrew C., through Creative Commons.

Figure 52. ***Stellaria humifusa***; members of this genus are eaten by several species of geese. Photo by Lynn J. Gillespie, through Creative Commons.

Figure 53. ***Carex aquatilis*** var. ***minor*** in water; members of this genus are eaten by several species of geese. Photo by Jeffery M. Saarela, through Creative Commons.

Figure 54. ***Branta leucopsis***, Barnacle Goose, grazing. This species grazes largely on mosses in the Arctic. Photo by Arthur Chapman, through Creative Commons.

Barnacle Geese (***Branta leucopsis***; Figure 54) arrive in Spitzbergen, Scandinavia, after a long migration, but before flowering plants are available (Prop & Vulink 1992). Thus mosses are eaten heavily during pre-laying and laying periods (62% in feces) (Fox & Bergersen 2005). The young goslings also consume the mosses, and sampling revealed that 27 out of 28 samples of adult and gosling droppings contained mosses (Prop & Vulink 1992). Snow Geese (***Chen caerulescens caerulescens***; Figure 50) and Pink-footed Geese (***Anser brachyrhynchus***; Figure 55) consume mosses to a lesser extent than the Barnacle Geese. It is interesting that moss in the diet increased as the temperature increased (Fox *et al*. 2006).

Figure 55. ***Anser brachyrhynchus***, Pink-footed Geese, foraging among grasses. Photo by Brian Eversham, with permission.

The Barnacle Goose (***Branta leucopsis***; Figure 54) grazes the top layer of mosses when the ***Calliergon*** (Figure 56) is still frozen (Prop & de Vries 1993). Along the water's edge, the geese dug for large lumps of mosses, consuming them as soon as they appeared. Fortunately, the mosses were a nearly inexhaustible food supply, but the geese seemed to prefer them when they were still anchored in ice. That made it possible for them to scrape the upper, most nutritious part with their bills without having to attempt separating them from their lower parts that were sealed in ice. Grasses began to grow when the moss beds began to thaw and within one week the young leaves appeared and were immediately consumed by the geese. During the earliest stages of this thaw, the geese fed on **forbs** (herbaceous flowering plant other than grass) and xerophytic mosses on the few snow-free patches. Then the forbs became the dominant food for about ten days. Then the moss meadows became available and the females switched to feeding on mosses, with their forbs proportion dropping to only 50%. As they became more available, graminoids gradually took on more importance in the diet of both males and females. However, at that time the proportion of mosses in the male diet was greater than that of females, both making great use of mosses in the moss meadows for food.

Figure 56. ***Calliergon cordifolium***, a genus that is grazed by Barnacle Geese (***Branta leucopsis***; Figure 54) when the moss is still encased in ice. Photo by Janice Glime.

One factor in determining suitable food is retention time (Prop & Vulink 1992). Since plant cell walls are difficult to digest, and bryophytes have a higher cell wall to cell content ratio, the bryophytes are more difficult to digest than herbaceous foods. The Barnacle Goose (***Branta leucopsis***; Figure 54) increased its retention time 2-4-fold as the short days of winter increased to the continuous light of summer in their Arctic breeding area. This permitted greater digestion of their food from 37% in winter to 56% in summer and allowed them to expand their food choices to include bryophytes – often the only food available in their summer range.

Competition may force some geese to eat mosses. When Barnacle Geese (***Branta leucopsis***; Figure 54) and Pink-footed Geese (***Anser brachyrhynchus***; Figure 55) coexist during molting time, their diet of sedges and grasses shifts to include more mosses, especially in the Barnacle Goose, reaching 33% of the diet, whereas mosses only reached 17% of the Pink-footed Goose diet (Madsen & Mortensen 1987). The Pink-footed Goose seems to be able to keep the Barnacle Goose from feeding in the preferred sedge and grass food patches. Mosses are suboptimal for both nutrients and fiber content compared to sedges and grasses.

Ardea and Sage (1982; Sage & Ardea 1982) note that the Barnacle Geese (***Branta leucopsis***; Figure 54) begin eating mosses as soon at they arrive in their Arctic breeding grounds. The authors suggest that this is necessary for them to build up **arachidonic acid**, a fatty acid in cell membranes. This notion is supported by Prins (1982). Several species of geese are known to eat mosses in their Arctic breeding grounds, including the Snow Goose (***Chen caerulescens***; Figure 50), Pink-footed Goose (***Anser brachyrhynchus***; Figure 55), Barnacle Goose, and Brant Goose (***Branta bernicla***; Figure 1). Prins suggested that the arachidonic acid helped to keep the membranes pliable as they move about on the frozen Arctic ground. The Canada Goose (***Branta canadensis***; Figure 47) instead eats horsetails (*Equisetum*; Figure 57), which are likewise rich in arachidonic acid, but mosses have the highest contents known.

Figure 57. *Equisetum arvense*, a source of arachidonic acid for Canada Goose (***Branta canadensis***). Photo by MPF, through Creative Commons.

When snow melt is delayed, as it has been recently along Hudson Bay shores, a predicted outcome of global warming, as many as 100,000 Snow Geese (***Chen caerulescens caerulescens***; Figure 50) stay for weeks instead of 1-2 days as in the past. The result is devastation of salt marsh and wetland plants, and only the moss carpet seems able to grow.

In the high Andes of sub-Antarctic South America, ***Attagis malouinus*** (White-bellied Seedsnipe; Figure 58), ***Chloephaga picta*** (Upland Goose; Figure 59), and ***C. poliocephala*** (Ashy-headed Geese; Figure 60) frequently consume bryophytes (Russo *et al* 2020). The fragments, including both leafy stems and capsules, occurred in 84.6% of the seedsnipe (26 samples) and 90.9% of the Chloephaga goose fecal samples (22 samples; Figure 61). At least one of the ***Chloephaga*** species consumes the mosses ***Polytrichum strictum*** (Figure 62) and ***Notoligotrichum trichodon*** (Figure 63). Of 11 collected goose droppings, more than 50% contained fragments of the **Polytrichaceae**. Such consumption suggests the possibility of dispersal of this moss family in bird feces.

Figure 58. ***Attagis malouinus*** in mountain area of Patagonia, a sub-Antarctic bird that eats mosses. Photo courtesy of Sebastian Saiter.

Figure 59. ***Chloephaga picta***, a sub-Antarctic bird that eats mosses. Photo by Peter Prokosch, through Creative Commons.

Figure 60. ***Chloephaga poliocephala***, sub-Antarctic bird that eats mosses on Ushuaia, Tierra del Fuego, Argentina. Photo through Creative Commons.

Figure 61. ***Chloephaga feces*** with mosses in it. Photo courtesy of Nick Russo, modified by Janice Glime.

Figure 62. Male plants of ***Polytrichum strictum***, a common food of ***Attagis malouinus***, ***Chloephaga picta***, and ***Chloephaga poliocephala***. Photo by Kristian Peters, through Creative Commons.

Figure 63. ***Notoligotrichum trichodon*** with capsules; both leafy stems and capsules are common foods of ***Attagis malouinus***, ***Chloephaga picta***, and ***Chloephaga poliocephala***. Photo by Bernard Goffinet, with permission.

Blood Pheasant

The Blood Pheasant (***Ithaginis cruentus***; **Phasianidae**; Figure 64) is protected in China, where it lives in shrublands on high, cold plateaus. Mosses are an important part of its diet (Shi & Li 1985; Nan *et al*. 2011). Yao (1992) dissected 46 gizzards to analyze for food preferences. This revealed 32 species of mosses, comprising 22 genera and 14 families. The preferred mosses comprised 24-54% of the content, second preference comprised 11-17%, third preference 4-9%, and those occasionally eaten comprised less than 2.1%.

Figure 64. ***Ithaginis cruentus***, Blood Pheasant, a species for which mosses are an important diet component. Photo from EOL China Regional Center, through Creative Commons.

Other foods of the Blood Pheasant include grasses, and both mosses and grasses are taken during prolonged feeding expeditions in which the birds bob up and down like a slow sewing machine needle at the rate of 50 pecks per minute (Nan *et al*. 2011). In 528 observations, all individuals consumed mosses. Although it was difficult to distinguish which bryophytes were being consumed, the researchers were able to identify ***Actinothuidium hookeri*** (Figure 65), ***Funaria hygrometrica*** (Figure 66), ***Hedwigia ciliata*** (Figure 67), ***Homomallium connexum*** (see Figure 68), ***Pogonatum perichaetiale*** (Figure 69), and ***Rhytidium rugosum*** (Figure 70). It appeared that the birds preferred mosses that were soft and easily fragmented for ease of swallowing. On the other hand, some of these mosses may help to grind food in the gizzard. Grasses were also eaten in large supply, but since they were abundant, it did not appear that the mosses served as emergency food or a source of fiber. Furthermore, it did not appear that the mosses were eaten as a source of insects because the insects were in low supply. Hence, it appears that the mosses were a preferred food.

Figure 65. ***Actinothuidium hookeri***, food of the Blood Pheasant (***Ithaaginis cruentus***). Photo by Li Zhang, with permission.

Figure 66. ***Funaria hygrometrica*** capsules, food for the Blood Pheasant. Photo by Frank Vincentz, through Creative Commons.

Figure 67. ***Hedwigia ciliata*** drying, a species eaten by the Blood Pheasant. Photo by Janice Glime.

Figure 68. ***Homomallium incurvatum***; ***H. connexum*** is among the mosses consumed by the Blood Pheasant. Photo by Hermann Schachner, through Wikiwand.

Figure 69. ***Pogonatum perichaetiale*** with capsules. This species is eaten by the Blood Pheasant. Photo by Li Zhang, with permission.

Figure 70. ***Rhytidium rugosum***, food for the Blood Pheasant. Photo by Michael Lüth, with permission.

Kakapo

On Stewart Island, the third largest island of New Zealand, the Kakapo (***Strigops habroptilus***; Figure 71) "plucks" the mast of the moss ***Dicranoloma*** (Figure 72), the sedge *Oreobolus*, the grass *Centrolepis*, the flowering plant *Astelia*, and the Asteraceae member *Celmesia* (Best 1984). Signs on ***Dicranoloma*** were rare, typically represented as foliage that had been pulled from the ground.

Figure 71. ***Strigops habroptilus***, Kakapo, camouflaged among leaves in NZ. The coloration camouflages it among the vegetation, including while it feeds among bryophytes. Photo by Mnolf, through Creative Commons.

Figure 72. ***Dicranoloma billardieri*** in NZ, a species often pulled up by the Kakapo. Photo by Jan-Peter Frahm.

Turkeys?

Glover and Bailey (1949) reported that turkey droppings indicated that bryophytes formed a common food source from January to April in the beech-birch-maple-hemlock forest. However, it appears that the "mosses" in this case were instead actually *Lycopodium*, referred to elsewhere in the paper as a bryophyte.

Dispersal

The birds in some cases return the "favor." The Mallard, ***Anas platyrhynchos*** (Figure 73) and Lapwing ***Vanellus vanellus*** (Figure 74) both eat bryophytes. Wilkinson *et al*. (2017) found a large fragment of the moss ***Didymodon insulanus*** (Figure 75) in the feces of the Mallard in Cumbria, England, and similarly in the Lapwing feces. These fragments were cultured and proved to be viable. This suggests that consumption of bryophytes by birds can in some cases be a means of dispersal. Could this be more true for species that benefit from guano deposits?

Figure 73. ***Anas platyrhynchos***, Mallards, birds that eat bryophytes. The mosses can remain live in the feces. Photo courtesy of Eileen Dumire.

Figure 74. ***Vanellus vanellus***, Northern Lapwing, a bird that consumes bryophytes. The bryophytes can remain viable in the feces. Photo by Andreas Trepte, through Creative Commons.

Figure 75. ***Didymodon insulanus***, a moss that can survive the digestive tract of Mallards and Lapwings Photo by David T. Holyoak, with permission.

Nutritional Value of Bryophytes

These records raise the question of nutritional value of bryophytes. Why do birds eat bryophytes? Sugawa (1960) found that puppies and chickens will eat the pendent moss ***Neodicladiella pendula*** that is pulverized and used as a food additive. These animals seemed to suffer no ill effects. In fact, they gained more weight than the controls. Sugawa found that these mosses contained considerable Vitamin B_2. Mosses can have high contents of vitamins, especially B_2 (Sugawa 1960; Margaris & Kalaitzakis 1974).

The greatest known use of bryophytes as food for birds occurs in the Arctic tundra. In these mosses, the caloric content is ~4.5-5.0 kcal g^{-1} (Pakarinen & Vitt 1974). The flowering plants consist of about 15% protein and 5% fats, whereas mosses have about 4% protein and 2% fats. Much of the moss biomass is bound in lignin-like compounds. Sugars in these mosses comprise ~1.5%. These sugars include mannose, melibiose, maltose, and deoxyribose in the mosses ***Syntrichia princeps*** (Figure 76), ***Rhynchostegium*** sp. (Figure 77), ***Platyhypnidium riparioides*** (Figure 78), and ***Homalothecium*** spp. (Figure 79) (Margaris & Kalaitzakis 1974).

Figure 76. ***Syntrichia princeps*** with capsules. Photo by Michael Lüth, with permission.

Figure 77. ***Rhynchostegium alopecuroides***. Photo by Michael Lüth, with permission.

Figure 78. ***Platyhypnidium riparioides*** with capsules, an emergent aquatic moss. Photo by Michael Lüth, with permission.

Figure 79. ***Homalothecium lutescens*** Europe 2 Michael Lüth, with permission.

Forman (1968) examined caloric values of thirteen bryophyte species from Mt. Washington, NH, USA. Values for fresh bryophytes varied from 3747 cal g^{-1} dry weight for ***Dicranella heteromalla*** (Figure 80) to 4305 cal g^{-1} in ***Thuidium delicatulum*** (Figure 81). But then, spinach has only 0.23 cal g^{-1} of fresh spinach (1 cup) (Wikipedia 2017). When species were transplanted to a high-temperature and high-humidity environment, the caloric content decreased. On the other hand, bryophyte species that originated from the coniferous and northern hardwoods forests all had higher caloric values than those from the higher alpine area or the lowland oak forest. On Mt. Washington, the bryophytes are among those plants with the lowest caloric values.

Mosses can affect the nutritional value of forbs and grasses in Arctic wetlands (Kotanen 2002). Moss presence did not prevent the rapid uptake of nitrogen by other forage species. However, most of added N nevertheless ended up in the moss layer. Hence, the mosses are able to divert N away from the tracheophyte forage plants and into long-lasting peat. This sequestering can make it more difficult for freshwater tracheophyte forage plants to recover from excessive foraging by Snow Geese (***Chen caerulescens atlantica***; see Figure 50). On the other side of the coin, the Snow Geese fertilize the moss layer in the polygon fens (Pouliot 2006).

Figure 80. ***Dicranella heteromalla***, a moss with ~3700 cal g^{-1} dry weight. Photo by Michael Lüth, with permission.

Figure 81. ***Thuidium delicatulum***, a moss with ~4300 cal g^{-1} dry weight. Photo by Michael Lüth, with permission.

Solheim *et al*. (1996) showed that grazing geese had a significant impact on nitrogen fixation in the Arctic Svalbard. In areas with grazing there was 10X as much N fixation as in areas with no grazing. Bird droppings under cliffs likewise increased N fixation.

Atmospheric pollutants are having a large impact on the N content of bryophytes. Pitcairn *et al*. (1995) found that atmospheric N deposition caused a significant rise in tissue N of 38% in central Scotland to 63% in Cumbria during just two decades.

Crafford and Chown (1991) suggested that herbivory by curculionid beetles on bryophytes originated in response to an absence of flowering plants during glacial periods. For birds, it appears that Arctic birds that eat bryophytes likewise have occupied a feeding niche that at least during part of the year is devoid of flowering plants.

Palatability

Bryologists for a long time assumed that bryophytes were inedible. This could result from bad taste, low nutrient value, or toxic effects. But, in fact, bryophytes are eaten. To humans they may taste terrible, with Crum (1973) describing ***Dicranum*** (Figure 82) as having a strong, somewhat peppery taste, ***Rhodobryum giganteum*** (Figure 83) as having a sickening sweet taste, and most tasting like raw green beans. But are these the tastes registered by the birds? Feeding preference tests of birds with choices of leafy bryophytes and capsules seem to be lacking. Are there species preferences? Does color matter? Do they provide some essential nutrient that is more abundant in bryophytes than in other foods?

Foraging

As already discussed in earlier chapters, many invertebrates reside among the bryophytes. These include grubs, beetles, bugs, worms, mites, spiders, and other macroinvertebrates. Many of these organisms are desirable food for birds. Hence, many birds forage among bryophytes, and some are specially adapted for this bryophyte foraging behavior.

Figure 82. ***Dicranum scoparium*** with capsules, a moss in a genus Crum described as tasting peppery. Photo by Janice Glime.

Figure 83. ***Rhodobryum giganteum***, a moss with a sickening sweet taste. Photo by David Long, with permission.

Ground Foragers

The Common Blackbird (***Turdus merula***; Figure 12) forages among mosses when snow still covers part of the ground (see film by Shutterstock 2017). It is likely that other early arrivals take advantage of the moss fauna when most insects are in the egg or pupal stage, often hidden under bark or in the soil and immobile.

Arctic Foraging Effects

In the Arctic breeding grounds, mosses are typically the dominant vegetation. The thickness of the moss mats influence the temperature of the underlying soil (van der Wal *et al*. 2001). Herbivores, including birds, can reduce that mat thickness by trampling, consumption, or foraging. When Barnacle Geese (***Branta leucopsis***; Figure 54) and reindeer were excluded from areas with moss cover at Spitsbergen, the moss mat increased in thickness and the soil temperature was reduced by 0.9°C. In all sites, the soil temperature was negatively correlated with the thickness of the moss mat. This temperature change had no effect on the moss growth rate, but the Arctic meadow-grass (***Poa arctica***; Figure 84) and polar cress [***Cardamine pratensis*** (= ***C. nymanii***); Figure 85] experienced a 50% reduction in biomass on the chilled soils.

Figure 84. ***Poa arctica***, an Arctic grass that diminishes in cover at lower temperatures. Photo by R. J. Soreng, through Creative Commons.

Figure 85. ***Cardamine pratensis***, a species that has less growth at lower soil temperatures. Photo by Aiwok through Creative Commons.

Arctic foraging can have detrimental effects on the plants in this fragile ecosystem, but at times they benefit the bryophytes. The Lesser Snow Goose (***Chen caerulescens caerulescens***; Figure 50) in the Arctic coastal region can be very destructive while foraging among roots and rhizomes for grubs and other food (Jefferies 1988). At the rate of foraging exhibited, Jeffries estimated that the sedge meadow would convert to a moss carpet in about five years.

Foraging on Epiphytes

Bryophytes are often torn up by foraging birds, presumably in search of insects and other invertebrates. In the Pacific Northwest, USA, 44% of the foraging among epiphytes was on bryophytes. These were mostly pendant bryophytes (Figure 86), followed by foliose lichens (Figure 87), then appressed bryophytes (Figure 88). In these forests, 20% of the bryophyte foraging was on the abundant moss ***Isothecium myosuroides*** (Figure 86). The bark insectivorous birds were the most frequent foraging guild on the bryophyte and lichen substrates.

Figure 86. ***Isothecium myosuroides***, most common epiphytic moss foraged by birds in the Pacific Northwest. Photo by Dale Vitt, with permission.

Figure 87. ***Flavoparmelia caperata***, a foliose lichen like those foraged by birds in the Pacific Northwest. Photo by Robert Klips, with permission.

Figure 88. ***Hypnum imponens*** on log, an appressed bryophyte like those that are less preferred for foraging by birds in the Pacific Northwest. Photo by Janice Glime.

As an example, we know that the Blue Tit (***Cyanistes caeruleus***; Figure 15) eats larvae of ***Erannis*** (Lepidoptera) in winter (Betts 1955) – a moth associated with forests with lots of bryophyte cover (Kiadaliri *et al*. 2005). Females of at least some species of ***Erannis*** lay eggs under mosses as well as in crevices, making this a good foraging site for birds hunting larvae.

Wolf (2009) questioned the value of epiphyte foraging to birds in coniferous forests of the Pacific Northwest. Of the 735 foraging records, ~30% occurred on epiphytic substrates. The data indicated selectivity by the Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89), Red-breasted Nuthatch (***Sitta canadensis***; Figure 90), Brown Creeper (***Certhia americana***; Figure 91), Hairy Woodpecker (***Picoides villosus***; Figure 92), and Gray Jay (***Perisoreus canadensis***; Figure 93). Furthermore, the position in the canopy influenced their choices. In the mid and upper crown, lichens were preferred, whereas in the lower crown the bryophytes were preferred. Weikel and Hayes (1999) suggested that the bryophyte cover may house more arthropods that serve as food, but at the same time they hide the arthropods, making them less available to these birds.

Figure 89. ***Poecile rufescens***, Chestnut-backed Chickadee, a species that typically forages among epiphytic bryophytes in the Pacific Northwest, USA. Photo by Walter Siegmund, through Creative Commons.

Figure 90. ***Sitta canadensis***, Red-breasted Nuthatch, a species that forages among epiphytic bryophytes in the Pacific Northwest. Photo by Matt MacGillivray, through Creative Commons.

Figure 91. ***Certhia americana***, Brown Creeper, on a tree where it often forages among mosses and lichens. Photo by Walter Siegmund, through Creative Commons.

In the Pacific Northwest coniferous forests of Washington and Oregon, USA, eleven species of birds use the bryophytes for foraging (Wolf 2009). However only four bird species comprised 79% of the foraging records. These were the Pacific Winter Wren (now named ***Troglodytes pacificus***; Figure 94; 33 records), Brown Creeper (***Certhia americana***; Figure 91; 13 records), Gray

Jay (***Perisoreus canadensis***; Figure 93; 14 records), and Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89; 13 records). Among these, the Brown Creeper (***Certhia americana***), Hermit Thrush (***Catharus guttatus***; Figure 95), and Winter Wren used the bryophytes in more than 20% of their foraging excursions.

Figure 92. ***Picoides villosus***, Hairy Woodpecker, a species that forages among epiphytic mosses. Photo by Will Pollard, through Creative Commons.

Figure 93. ***Perisoreus canadensis***, Gray Jay, a species that forages among epiphytic bryophytes. Photo by Franco Folini, through Creative Commons.

Figure 94. ***Troglodytes pacificus***, Pacific Wren, a forager among bryophytes. Photo by Carly Lesser & Art Drauglis, through Creative Commons.

Figure 95. ***Catharus guttatus***, Hermit Thrush, a species that frequently forages among bryophytes. Photo by Cephas, through Creative Commons.

The behavior differed among these birds (Wolf 2009). The Brown Creeper (***Certhia americana***; Figure 91) and Hairy Woodpecker (***Picoides villosus***; Figure 92) hung vertically or upside-down on the epiphytes as they probed, hammered, pecked, or otherwise inspected the epiphytic bryophytes, using mostly prostrate mosses (esp. ***Hypnum***; Figure 96) on the bole. The arthropods that are the victims of their searches use the epiphytes for refuge, forage, rest, aestivation, and thermoregulation (Richardson & Young 1977; Rhoades 1995; Shaw 2004). The dense mats accumulate soil, providing further habitat for invertebrates (Winchester & Ring 1996). The birds contribute a selection pressure that selects for cryptic coloration and other forms of camouflage in the arthropods (Richardson & Young 1977).

Figure 96. ***Hypnum cupressiforme***, a common epiphytic genus for foraging by Brown Creepers and Hairy Woodpeckers. Photo by Jan-Peter Frahm, with permission.

With the wide range of bryophytes in the Neotropics, certainly some are better sources of food items than others. The Ochraceous Wren and Common Bush-Tanager forage among the dead organic matter and bryophytes more frequently than they do among other (tracheophyte) epiphytes (Nadkarni & Matelson 1989).

In Costa Rica, The Ruddy Treerunner (***Margarornis rubiginosus***; Figure 97) is an epiphyte specialist, foraging on bryophytes (Sillett 1994). The Spot-crowned Woodcreeper (***Lepidocolaptes affinis***; Figure 98) is a Central American foraging specialist on bryophytes and foliose lichens, but the bryophytes were used less proportionately than lichens.

Figure 97. ***Margarornis rubiginosus***, Ruddy Treerunner, a species that specializes on foraging among bryophytes. Photo by Dominic Sherony, through Creative Commons.

Figure 98. ***Lepidocolaptes affinis***, Spot-crowned Woodcreeper, foraging among mosses. Photo by Carmelo López Abad, through Creative Commons.

The Blue-capped Ifrita (***Ifrita kowaldi***; Figure 99), a poisonous bird, is restricted to the highlands of New Guinea (Figure 100), mostly above 2000 m asl (Dumbacher *et al*. 2000). They live in mossy, moist montane forests, where they behave much like the nuthatches, foraging for insects and worms among mosses, on tree trunks, and on major branches in the midstory of the forest. They are rarely seen alone, typically travelling in groups of up to six individuals.

Figure 99. Blue-capped Ifrita, ***Ifrita kowaldi***, a poisonous bird that lives in mossy forests where it forages among midstory mosses. Photo by Jerry Oldenettel, through Creative Commons.

Figure 100. New Guinea Highlands, Papua New Guinea. Photo from eGuide Travel, through Creative Commons.

Pendant bryophytes (Figure 101) can protect some arthropods from foragers. These arthropods are able to dwell at some distance from the branch, away from the perches of the birds (Wolf 2009). These mosses are too unstable for many kinds of birds to perch. Among the birds that were not deterred by the pendant branches, the Pacific-slope Flycatcher (***Empidonax difficilis***; Figure 102) used a sally, hover, and glean foraging behavior to capture insects on the dangling bryophytes. The Chestnut-backed Chickadee (***Poecile rufescens***; Figure 89) used short flights and hops to forage, but occasionally hovered or hung from the bryophytes to snatch an insect from the pendant portion. Furthermore, 70% of the nests of this species contained bryophytes (Dahlsten *et al*. 2002).

Peterson *et al*. (1989) sampled trunk-surface arthropods from American beech (*Fagus grandifolia*; Figure 103) and sugar maple (*Acer saccharum*; Figure 104). The arthropod resources did not differ significantly between trees. Furthermore, they were not correlated with bark texture or bryophyte cover.

Figure 101. ***Pseudobarbella mollisima***, a pendant moss in Japan. Photo by Janice Glime.

Figure 102. ***Empidonax difficilis***, Pacific-slope Flycatcher, a species that is able to forage among dangling mosses. Photo by Ron Knight, through Creative Commons.

Figure 103. *Fagus grandifolia* forest in winter. Photo by Dcrjsr, through Creative Commons.

Pheasants (***Phasianus colchicus***; Figure 105) do not seem to have any particular use for the mosses themselves, but the mosses seem to be in their way on the forest floor of a wetland forest (Wiegers 1983). When they are foraging, they turn the bryophyte cover upside down in search of food. Following these events, some mosses, including ***Dicranum scoparium*** (Figure 106) and ***Mnium hornum*** (Figure 107), that were turned upside down develop into moss balls.

Figure 104. *Acer saccharum* autumn leaves and trunk. Photo by Janice Glime.

Figure 105. ***Phasianus colchicus***, Pheasant, a species that often disturbs bryophytes while foraging. Photo by Gary Noon, through Creative Commons.

Figure 106. ***Dicranum scoparium***, a moss that gets turned upside down by foraging pheasants. Photo by J. C. Schou, through Creative Commons.

Rod Seppelt (Bryonet 26 February 2013) has observed Skuas (***Catharacta lonnbergi***; Figure 108) upturning upland moss polsters of ***Ditrichum strictum*** (see Figure 109) on subAntarctic islands, searching for earthworms. It is puzzling because there are easier food items available than these relatively small worms.

Figure 107. ***Mnium hornum***, a moss that gets turned upside down by foraging pheasants. Photo by Kristian Peters, through Creative Commons.

Figure 108. ***Catharacta lonnbergi***, Skua, on nest on South Georgia, a species that upturns mosses to forage. Photo by Christo Barrs, through Creative Commons.

Figure 109. ***Ditrichum gracile***; ***D. strictum*** is commonly upturned by foraging Skuas on sub-Antarctic islands. Photo by Hermann Schachner, through Creative Commons.

In Eugene, Oregon, USA, the Steller's Jay (***Cyanocitta stelleri***; Figure 110) tears up mosses from the oaks as it forages for arthropods that hide there (Wagner 2013). In other locations it is Crows (Figure 112) and Scrub Jays (***Aphelocoma californica***; Figure 111).

Figure 110. ***Cyanocitta stelleri***, Steller's Jay, a species that forages on mosses on oaks in the Pacific Northwest, USA. Photo by Alan D. Wilson, through Creative Commons.

Figure 111. ***Aphelocoma californica***, Scrub Jay, a species that tears up mosses on oak trees. Photo by Minette Layne, through Creative Commons.

Crows (***Corvus***; Figure 112) are among those birds that can be quite destructive to bryophytes. Erkamo (1976) reported that some animal had upturned mosses on flat, open rocks in Finland. These mosses were typically only a few cm across, but some were up to 10-15 cm. Since the observations are indirect, based only on the upturned mosses, it is possible that voles, pheasants, seagulls, or crows were responsible, but crows seemed most likely. Erkamo has, at other times, seen crows engaging in such activity, presumably searching for insects or worms.

Birds keep bryophytes from growing well on red wood ant (***Formica rufa*** group; Figure 113) mounds due to the bird foraging activity on the ants (Heinken *et al*. 2007).

Motley and Bosanquet (2004) reported a neglected flower pot that contained ***Petalophyllum ralfsii*** (Figure 114). Meanwhile, the surface had been colonized by various species of moss and the thallose liverwort ***Aneura***

(Figure 115). The surprise came when birds attacked the bryophytes, pulling them out and most likely taking them for nesting material. But they were selective. They avoided taking the ***P. ralfsii***.

Figure 112. ***Corvus corax***, Crow, a species that is destructive of bryophytes while foraging. Photo by Ingrid Taylar, through Creative Commons.

Figure 113. ***Formica rufa*** sideview, an ant that builds mounds and birds keep bryophytes from growing on them. Photo by Richard Bartz, through Creative Commons.

Figure 114. ***Petalophyllum ralphsii***, a species that is avoided when birds collect bryophytes for nests. Photo by Michael Lüth, with permission.

Figure 115. ***Aneura pinguis***, a bryophyte among those collected by birds, presumably for nesting material. Photo by Michael Lüth, with permission.

Juncos

The Dark-eyed Junco (***Junco hyemalis***; Figure 116) in the Pacific Northwest, USA, is most active in the low understory, but it may go to the upper canopy to search for prey items among the lichens (Wolf 2009). But they may also forage on ***Dicranum*** sp. (Figure 82, Figure 106) and ***Isothecium*** (Figure 86), where Wolf observed them on a horizontal tree bole and branch of *Tsuga heterophylla* (Figure 117) at 0.7 m and 3 m respectively.

Figure 116. ***Junco hyemalis***, Dark-eyed Junco, a species that forages on ***Dicranum*** sp. and ***Isothecium***. Photo by Factumquintus, through Creative Commons.

Figure 117. ***Tsuga heterophylla*** (hemlock) forest, home of the Dark-eyed Junco. Photo by Willow & Monk, through Creative Commons.

Weaver Birds

In the Udzungwa Mountains of Tanzania, the disturbed humid forest serves as home for at least 70 species of birds (Fjeldså 1999). Many of the birds search for their food among the epiphytic lichens, mosses, and ferns in the mature forests. The Tasmanian Mountain Weaver, ***Ploceus nicolli*** (Figure 118), is a vulnerable species that occurs in the tall forest of the Eastern Arc Mountains. It is associated with locations having large cover of epiphytic mosses and lichens.

Figure 118. ***Ploceus velatus***, Southern Masked Weaver and nest; ***P. nicolli*** lives in areas with a large cover of epiphytic mosses. Photo by Chris Eason, through Creative Commons.

Tropical Birds

In the tropics, some birds use epiphytes as their feeding substrates. These include at one end of the spectrum those birds that choose the substrate where they prefer to feed, and at the other end the birds choose the prey item, going to the substrate if it potentially has that prey organism. In Costa Rica, Sillett (1994) studied eight species that use epiphytes among their feeding substrates. Four species were epiphyte specialists. These included two that chose bryophytes: Ruddy Treerunner (***Margarornis rubiginosus***; **Furnariidae**; Figure 97) on just bryophytes and Spot-crowned Woodcreeper (***Lepidocolaptes affinis***; **Dendrocolaptidae**; Figure 98) on bryophytes and lichens.

Orians (1969) and Remsen (1985) have provided evidence of bryophyte utilization by tropical birds, but otherwise, little documentation of this tropical resource exists. In Neotropical Costa Rica, Nadkarni and Matelson (1989) report three birds that feed upon bryophyte inhabitants (Table 1). The Emerald-chinned Hummingbird (***Abeillia abeillei***; Figure 119) and Amethyst-throated Hummingbird (***Lampornis amethystinus***; Figure 120) feed upon insects associated with the mosses and other bryophytes. The Rufous-tailed Hummingbird (***Amazilia tzacatl***; Figure 121) utilizes the flowers that are anchored in the bryophytic substrate. In fact, the Ochraceous Wren (***Troglodytes ochraceus***; Figure 122) and Common Bush-Tanager (***Chlorospingus ophthalmicus***; Figure 123) foraged in mosses more frequently than expected. Avian resources nestled among the bryophyte mats include fruits, flowers, seeds, water, and invertebrates.

Table 1. Percentage (and total number) of foraging visits to epiphytes by birds that probed moss mats and dead organic matter in the Monteverde field study, 1 July to 28 August 1985. Frequent foragers had 10 or more foraging visits recorded during the study period. Infrequent foragers had less than 10 foraging visits recorded. From Nadkarni and Matelson (1989).

Frequent foraging visits (> 10 foraging visits)	
White-throated Mountain-gem, *Lampornis castaneoventris*	95 (150)
Ochraceous Wren, *Troglodytes ochraceus*	89 (19)
Common Bush anager, *Chlorospingur ophthalmicus*	57 (511)
Olive-striped Flycatcher, *Mionectes olivaceus*	46 (37)
Slate-throated Redstart, *Myioborus miniatus*	45 (47)
Prong-billed Barbet, *Semnornis fiantzii*	30 (23)
Golden-browed Chlorophonia, *Chlorophonia callophrys*	33 (187)
House Wren, *Troglodytes aedon*	26 (57)
Three-striped Warbler, *Basileuterus tristriatus*	20 (10)
Mountain Robin, *Turdus plebejus*	< 10 (146)
Infrequent foragers (< 10 total foraging visits)	
Spotted Barbtail, *Premnoplex brunnescens*	

Figure 119. ***Abeillia abeillei***, Emerald-chinned Hummingbird, a tropical bird that feeds on insects associated with bryophytes. Photo by Scott Bowers, through Creative Commons.

Figure 120. ***Lampornis amethystinus***, Amethyst-throated Hummingbird, a tropical bird that feeds on insects associated with bryophytes. Photo by Juan Carlos Pérez M., through Creative Commons.

Figure 121. ***Amazilia tzacatl***, Rufous-tailed Hummingbird, a bird that feeds on flowers that are anchored in bryophytes. Photo by Brian Gratwicke Creative Commons.

Figure 122. ***Troglodytes ochraceus***, Ochraceous Wren, on mosses, a location where it forages. Photo by Annika Lindqvist, through Creative Commons.

Figure 123. ***Chlorospingus ophthalmicus***, Common Bush Tanager, on bryophytes where it forages. Photo by Cephas, through Creative Commons.

In subtropical evergreen forests, Dinesen (1995, 1997) reported on Shelley's Greenbul (***Arizelocichla masukuensis***; Figure 124). These birds found most of their food among the epiphytic mosses.

Figure 124. Shelley´s Greenbul, ***Arizelocichla masukuensis***, a species that forages among epiphytic mosses. Photo by Per Holmen, with permission.

Jamaican Blackbird

Another tropical bird, the Jamaican Blackbird, ***Nesopsar nigerrimus*** (Figure 125), lives in the moist montane of Jamaica above 515 m (Cruz 1978). Its food includes insects, and its foraging behavior among the epiphytes, dead leaves, and moss-covered tree trunks and branches seems to be part of its adaptive evolution on the island. Its shorter legs, more curved claws, and longer, narrower bill adapt it for arboreal rummaging in crevices and among bryophytes.

Figure 125. ***Nesopsar nigerrimus***, Jamaican Blackbird, foraging amid lichens. Photo by Dominic Sherony, through Creative Commons.

Summary

Both capsules and leafy portions of bryophytes are eaten by some birds. This is particularly true in polar climates where tracheophytes are scarce or absent. These birds include grouse and pheasants, as well as

song birds. Even some parrots feed on capsules of ***Polytrichum***. In tundra regions, the ptarmigan and grouse chicks often depend on bryophytes, especially the high quality food of capsules. Some birds use bryophyte capsules as emergency food, and one might describe all use of bryophytes as emergency food, although in some habitats, the emergency is long-lived. This capsule feeding can be seasonal, can depend on a bad year for tracheophytes, or can be used in a habitat with low productivity.

Use of color by birds to locate food is a topic wide open for research. Several hypotheses have suggested that members of the **Splachnaceae** with their brightly colored capsules and fruity odors may get dispersed as a result of attracting birds. This may also occur for the moss ***Pleurophascum***. The ability of most songbirds and some others may enable the birds to see UV reflections that we have not discovered for capsules, or to locate bulbils and other bryophyte structures.

Leafy plants may be eaten as well, including by some diving birds and ptarmigans. Blood Pheasants, in particular, seem to consume large quantities of leafy bryophytes. In other cases, antiherbivory compounds keep the birds away, protecting the invertebrates living among the bryophyte branches. On the other hand, bryophytes may provide high concentrations of some vitamins, and one study on caloric content indicates that levels in leafy bryophytes may be high. Bryophytes can compete for nutrients, especially nitrogen, making the forbs less nutritious. Some birds may use the bryophytes to obtain arachidonic acid in preparation for winter.

The high ratio of cell wall to cell contents requires a long retention time of consumed bryophytes. This can reduce the feeding rate, causing the birds to remain quiet and less conspicuous. On the other hand, it might provide the bryophytes with a means of long-distance dispersal; some bryophytes survive passage through the digestive tract.

Perhaps the greatest food contribution of the bryophytes is through foraging. Many invertebrates reside there. This can be good or bad for the birds, with some specializing on bryophyte foraging and others unable to locate the invertebrates hidden by the bryophytes. Among these, the hanging bryophytes require the greatest specialization by the bird foragers, thus providing a safe haven for many invertebrates. On the other hand, the birds disturb the bryophytes on the ground and elsewhere, providing possible dispersal.

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