CHAPTER 16-1
BIRDS AND BRYOPHYTES INTERSECT

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Figure 1. ***Lepidocolaptes affinis***, Spot-crowned Woodcreeper, a bird that specializes on foraging among bryophytes and lichens, especially epiphytes such as these. Photo by Larry Thompson, through DiscoverLife <www.discoverlife.org>.

Where Birds and Bryophytes Intersect

Bryophytes, including epiphytes (Figure 1), form an important source of food and habitat for many birds in the tropical rainforests (Gradstein *et al*. 1996). Nadkarni (1994) considered that the epiphytes contributed to the diversity of birds by adding to the resources available, providing more opportunities for resource specialization, and spread the available resources in the canopy throughout the year. These included retention of nutrients in the canopy, providing habitat for invertebrates, and providing a foraging substrate in the canopy (Nadkarni *et al*. 2004).

There is a positive relationship between bryophytes, vascular plants, and breeding birds in marginal habitats bordering agricultural areas (Wuczyński *et al*. 2014). A study in Lower Silesia, Poland, revealed 47 species of birds and 90 of bryophytes in 70 of these marginal habitats. These numbers were topped by 414 species of tracheophytes. The number of species of bryophytes was positively correlated with the number of species of breeding pairs of birds. These relationships suggest that bryophytes are good biodiversity indicators and can be used as a surrogate taxon for overall species richness. But do the birds use the bryophytes in some way, or do both simply like the same habitats? Bryophyte species richness was significantly correlated with the number of trees and shrubs, explaining 49% of the variability.

Birds have the potential to play a major role in bryophyte use and dispersal (Takaki 1957). It only took me a short time to realize how destructive my finches were to the mosses in my garden room due to their continuous nest-building activities.

Some interactions with mosses may not even involve use of the mosses. Davis (1981) reports that Skuas on Signy Island in the maritime Antarctic were disruptive to the moss community because of their activities there. Once the Skuas have pulled up the mosses, the wind will transport them elsewhere.

Bryophytes also provide microclimate buffers, offering thermal protection (Wolf 2009). This not only provides an ameliorated "climate" for birds' feet, but also affects their food organisms living under and in the bryophyte mat.

Unfortunately, observer location introduces bias into the sampling (Wolf 2009). Ground-level birds were more difficult to observe. The presence of bryophytes, lichens, and **Cyanobacteria** increases the roughness of the canopy. This microtopography provides important ecological functions that include nesting and foraging. In the Pacific Northwest states of Oregon and Washington, 100 bird species breed in the coniferous forests, using bryophytes, lichens, or mistletoe among construction materials in their nests. In North America, nearly 40% of the 262 bird species use either lichens or bryophytes in their nests. In the coniferous forests of Oregon and Washington, 65% use lichens or bryophytes, and 45 species use both. Wolf argues for the maintenance of old-growth forests to support these relationships.

Even the Northern Spotted Owl (***Strix occidentalis caurina***; Figure 2) depends on bryophyte and lichen epiphytes because this owl eats the northern flying squirrel (***Glaucomys sabrinus***; Figure 3), a species that depends on lichens and mosses extensively for both food and nesting materials (FEMAT 1993).

Figure 2. ***Strix occidentalis caurina***, Northern Spotted Owl , a species that benefits from mosses because they eat northern flying squirrels that feed on and make nests with mosses. Photo from Bureau of Land Management, through Creative Commons.

Figure 3. ***Glaucomys sabrinus***, the northern flying squirrel that uses mosses for food and nesting, but then itself becomes food for the Northern Spotted Owl. Photo by Bob Cherry, through public domain.

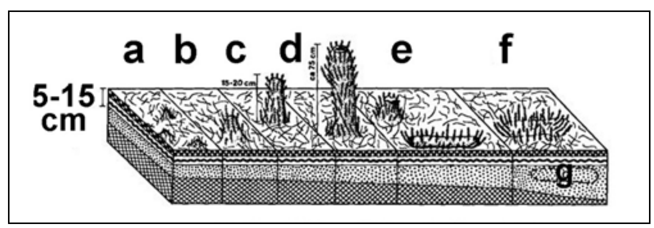

Figure 4. Developmental stages of bird watchtowers made of bryophytes. **a**. moss hummocks among morasses; **b.** early developmental stage of tower; **c.** immature tower; **d.** tower at optimum development stage; **e.** tower after collapse; **f.** collapsed tower overgrown by ***Polytrichum*** shoots; **g.** tower fragment remaining in peat. Modified from Kuc 1996.

Watch Towers and Sentinels

If you search for information on birds and watch towers, you are likely to find many articles on dangers of tall buildings, towers, and windmills to birds in flight. But in the tundra, where topography can be somewhat monotonous due to lack of trees and vertical structure, some birds use watch towers that they construct or that occur naturally in the landscape (Figure 4; Kuc 1996). And some of these birds use mosses as watch towers (Figure 5-Figure 6). This is known on Insla Grande de Tierra del Fuego, but mounds of mosses are likely used elsewhere as well.

Spending time on these towers detracts from the time spent foraging and thus is a tradeoff (Metcalfe & Furness 1984; Wickler 1985). The importance depends in part on how conspicuous the bird is and on the hunting tactics of the predators (Lendrem 1983a, b). The cost of this vigilance is reduced when it is shared with other birds, including those of other species (Metcalfe 1984; Sullivan 1984).

Hollén *et al*. (2008) demonstrated that in the Pied Babblers (***Turdoides bicolor***; Figure 7) the foragers gain more weight when these sentinels are in cooperative calling groups.

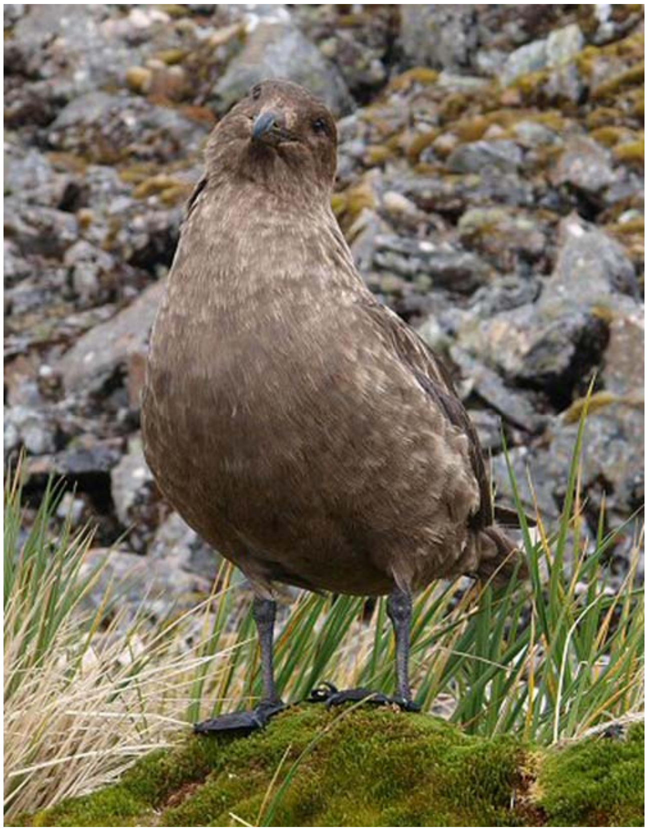

Figure 5. ***Stercorarius antarcticus***, Antarctic Skua sentinel on moss mound on South Georgia. Photo by Roger S. Key, with permission.

Figure 6. ***Anas georgica georgica*** (Yellow-billed Pintail), foraging while another is on a moss mound as a sentinel on South Georgia in the Antarctic. Photo by Roger S. Key, with permission.

Bathing

But bath mats? Appressed bryophytes on branches and limbs of trees provide bathing opportunities in the canopy, escaping the predators on the forest floor. One adult male Pacific Wren (***Troglodytes pacificus***; Figure 8) was using the mat of ***Dicranum*** spp. (Figure 9) 1.5 m above ground for his private bath, dipping into the creek beneath repeatedly, then rubbing his head and plumage into the moss to preen his feathers. But the moss was also wet, saturated by heavy fog in the morning. Winter Wrens (***Troglodytes troglodytes***; Figure 10) in Europe (now considered a separate species from those in North America) also bathe in dew-covered vegetation (Armstrong 1955). In Amazonia, the Conures (Figure 11), a kind of parrot in the subfamily **Arinae**, bathe communally in wet moss mats 23 m above the forest floor (Brightsmith 1999). Even the pelican may use mosses as a bathmat (Figure 12).

Figure 7. ***Turdoides bicolor***, Southern Pied Babbler. Photo by Derek Keats, through Creative Commons.

Figure 8. ***Troglodytes pacificus***, Pacific Wren, a bird that uses mosses as a bath mat. Photo by Upupa4me, through Creative Commons.

Figure 9. ***Dicranum scoparium***, a potential "bath mat" for the Pacific Wren. Photo by Misha Ignatov, with permission.

Figure 10. ***Troglodytes troglodytes***, European Winter Wren. Photo from Oskare Photography, through Creative Commons.

Figure 11. ***Aratinga solstitialis***, Sun Conure (**Arinae**), a Conure that might bathe in wet moss mats. Photo by Anshu, through Creative Commons.

Figure 12. Pelican drying on moss. Photo by Kapa, through public domain.

Thirsty Birds

Sometimes the mosses are the best source of a drink of water. In the Sandwich Isles of Hawaii, the Hawaii Mamo (***Drepanis pacifica***; Figure 13) obtains water from the epiphytic mosses, using rapid darts of the tongue on the wet mosses (Perkins 1903). The stomach contained no insects, so that could not explain the behavior.

Figure 13. ***Drepanis pacifica***, Hawaii Mamo, a bird that obtains water from epiphytic mosses. Photo by Hiart, through Creative Commons.

Fertilizer Effects of Birds on Bryophytes

Owls have yet another effect on bryophytes. Owl perches in Alaska provide a unique habitat for a few not-so-unique mosses: ***Bryum argenteum*** (Figure 14), ***Dicranum elongatum*** (Figure 15), ***Orthotrichum speciosum*** (Figure 16), and ***Syntrichia ruralis*** (Figure 17) (Steere 1976).

Figure 14. ***Bryum argenteum*** with capsules, a moss that can live on owl perches in Alaska. Photo by Ivanov, with permission.

Figure 15. ***Dicranum elongatum***, a moss that can grow on owl perches in Alaska. Photo by Michael Lüth, with permission.

Figure 16. ***Orthotrichum speciosum***, an epiphytic moss that can grow on owl perches in Alaska. Photo by Michael Lüth, with permission.

Figure 17. ***Syntrichia ruralis***, a species that can grow on owl perches in Alaska. Photo by David Holyoak, with permission.

Similarly, in Svalbard the "manuring" causes production of moss carpets that have a thin active layer (Vanderpuye *et al*. 2002). Beneath that is an accumulation of thick peat with no standing water. These manure deposits from the seabirds provides needed nutrients in this low-nutrient habitat.

Aplodon wormskioldii (**Splachnaceae**; Figure 18), includes owl pellets (Figure 19) among its substrates (Koponen 1990). Owl pellets are not guano, but rather are the regurgitated mass of indigestible materials.

Figure 18. ***Aplodon wormskioldii*** in Spitzbergen, a species that includes owl pellets among its substrates. Photo by Michael Lüth, with permission.

Figure 19. Owl pellet, substrate for ***Aplodon wormskioldii*** in Alaska. Photo by Gail Hampshire, through Creative Commons.

In the more temperate UK, Ken Adams (20 February 2014) reports on a ***Metzgeria violacea*** (Figure 20) on the side of a *Crataegus* bough. This location was so dense in a blackthorn bower that he supposed it could only have been introduced on a bird's foot. Air movement in the valley was too restricted to imagine that it had arrived that way. Recalling that ***Ulota phyllantha*** (Figure 21) supposedly prefers the nitrogen-rich bird droppings, he mused that this could be a similar situation. Or are these bryophytes simply tolerant of the droppings. It could also be that gemmae are simply deposited on branches where the birds perch. We know little of these relationships in the temperate zone.

Figure 20. ***Metzgeria violacea***, a species that might be dispersed by birds and may benefit from the guano. Photo by David Holyoak, with permission.

Figure 21. ***Ulota phyllantha***, a species that might be dispersed by birds and possibly benefit from the guano. Photo by Janice Glime.

Guano

Some birds favor certain mosses by large quantities of **guano** (accumulation of feces). Some seabirds tend to choose certain cliffs for roosting and defecating. The resulting **guano** (Figure 23) is high in some nutrients and provides the ideal substrate for its own unique flora. Among these plants are a number of **ornithocoprophilous** bryophytes – those that grow on bird dung. The most common of these include ***Ceratodon purpureus*** (Figure 22), ***Eurhynchium praelongum*** (Figure 24), and ***Mnium hornum*** (Figure 25), all species with a wide ecological amplitude (Watson 1964).

Figure 22. ***Ceratodon purpureus*** with capsules, a species that is able to grow on and may benefit from bird dung. Photo by Michael Lüth, with permission.

Figure 23. Guano of gulls and puffins on Farne Islands. Photo by Matthew Wills, through Creative Commons.

Figure 24. ***Eurhynchium praelongum***, a species that is able to grow on and may benefit from bird dung. Photo by Blanka Shaw, with permission.

Figure 25. ***Mnium hornum***, a species that is able to grow on and may benefit from bird dung. Photo by Des Callahan, with permission.

On Svalbard, near the Arctic Circle, Kuc (1996) reported an interesting relationship between the bryophytes and the Parasitic Jaeger (***Stercorarius parasiticus***; Figure 26). In the Nornsund Area, the moss ***Syntrichia ruralis*** (Figure 17) forms dense, high tufts in rings immediately

adjacent to the nests. Likewise, the moss ***Drepanocladus exannulatus*** (Figure 27), another dominant species, surrounded the nests, but in some areas this species was significantly degraded by the activities of the Parasitic Jaeger. In the dry tundra, the terrain was dominated by the moss ***Racomitrium lanuginosum*** (Figure 28-Figure 29), a moss that was heavily fertilized by guano from the Parasitic Jaeger.

Figure 26. ***Stercorarius parasiticus***, Arctic Jaeger, a species that seems to encourage the growth of ***Syntrichia ruralis*** near its nest. Photo by Donald Macauley, through Creative Commons.

Figure 27. ***Drepanocladus exannulatus***, a species common near the nests of the Arctic Jaeger (***Stercorarius parasiticus***), but that suffers from their activity. Photo by Michael Lüth, with permission.

Figure 28. ***Racomitrium*** in Iceland, a moss that is often fertilized by the Arctic Jaeger. Photo by Janice Glime.

Figure 29. ***Racomitrium lanuginosum***, a common species that lives in the tundra where the Arctic Jaeger provides it with a heavy fertilization by guano. Photo by Juan Larrain, with permission.

Megaphorura arctica (Figure 30), an Arctic springtail, feeds on a variety of bryophyte species (Hodkinson *et al.* 1994). These springtails form dense aggregates under bird cliffs, presumably benefitting from the guano, perhaps indirectly through the bryophytes. The bryophytes include ***Sanionia uncinata*** (Figure 31), ***Polytrichastrum alpinum*** (Figure 32), and ***Racomitrium lanuginosum*** (Figure 29).

The most fascinating association of bryophytes with bird droppings is that of some members of **Splachnaceae**. The moss ***Tayloria dubyi*** (Figure 33) seems to live exclusively on bird dung in the subAntarctic Magallanes ecoregion (Jofre *et al*. 2011). In fact, it may be restricted to the dung of the Upland Goose, ***Chloephaga picta*** (Figure 34).

Figure 30. ***Megaphorura arctica***, a springtail that lives among mosses under cliffs where guano drips. Photo by Arne Fjellberg, through Creative Commons.

Figure 31. ***Sanionia uncinata***, a moss that seems to benefit from bird drippings on cliffs. Photo by Michael Lüth, with permission.

Figure 32. ***Polytrichastrum alpinum***, a moss that lives under bird drippings on cliffs. Photo by Michael Lüth, with permission.

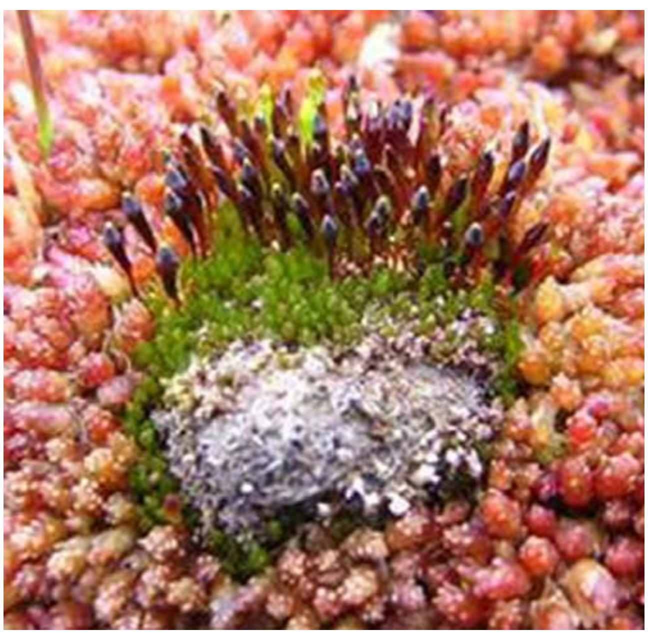

Figure 33. ***Tayloria dubyi*** with capsules, a species that lives on bird dung, especially of the Upland Goose, in the subAntarctic Magallanes ecoregion. Photo by Jocelyn Jofré, through Creative Commons.

Figure 34. ***Chloephaga picta***, Upland Goose, the bird whose dung provides the substrate for ***Tayloria dubyi*** in the subAntarctic. Photo by Fabien Dany <www.fabiendany.com>, with online permission.

But not all guano benefits are restricted to polar regions. In western North Carolina, USA, it is not the seabirds bringing oceanic nutrients to the cliffs, but rather nitrogen sources originate in the highly productive forests and are transferred to nutrient-poor terrestrial cliffs by birds (Langevin 2015). Among these, in particular, are common Ravens (***Corvus corax***; Figure 35) and Peregrine Falcons (***Falco peregrinus***; Figure 36). These birds frequently nest on cliffs in the southern Appalachian Mountains, excreting N-rich guano that increases the nitrogen below the nesting sites. Langevin showed that the ammonia levels were significantly higher below the nest sites. Likewise, there was a significant difference in vegetation, with particular lichens known to prefer high N being more common there. Beneficial effects of these forest N sources on bryophytes remain to be documented.

Figure 35. ***Corvus corax***, Raven, a species that brings nutrients from rich forests to cliffs where the nutrients are deposited as guano. Photo by Ingrid Taylar, through Creative Commons.

Figure 36. ***Falco peregrinus***, Peregrine Falcon and guano on cliff edge where it perches. Photo by Mike Baird through Creative Commons.

But guano does not always favor the mosses. In the polar Mac. Robertson Land, guano has reached toxic levels, making the coastal slopes barren of mosses and lichens (Bergstrom & Seppelt 1990). This is largely due to Antarctic Petrels (***Thalassoica antarctica***; Figure 37) that breed along these slopes, with a mean nest density of 0.82 m^{-1} (Alonso *et al.* 1987)! But the area also serves as breeding grounds for Southern Fulmars (***Fulmarus glacialoides***; Figure 38) and Adélie Penguins (***Pygoscelis adeliae***; Figure 39).

Figure 37. ***Thalassoica antarctica***, Antarctic Petrel flying. Photo by François Guerraz, through Creative Commons.

Figure 38. ***Fulmarus glacialoides***, Antarctic Fulmar roosting; their guano prevents establishment of bryophytes. Photo by Samuel Blanc, through Creative Commons.

Penguins

Penguins deserve special note because of their extensive role in N transfer from rich oceanic sources to land in the Antarctic. Cocks *et al.* (1998) reported a range of 13.1-25.9% of the Antarctic N to be from seabird guano, with similar results in other studies (Erskine *et al.* 1998; Bokhorst *et al.* 2007a, b; Lee *et al.* 2009). Wasley *et al.* (2012) interpreted this input to be from ancient penguin rookeries (Figure 39) that have been abandoned for thousands of years (Emslie & Woehler 2005). Bryophytes have elevated δ15N signatures (>15%), indicating their use of animal-derived N through repeated trophic transfer by microbial activity since the original deposition.

Figure 39. ***Pygoscelis adeliae***, Adelie Penguin on Antarctica, illustrating the large number of birds that can create guano. Photo by Murray Foubister, with permission

In the case of the Adelie Penguin (***Pygoscelis adeliae***; Figure 39), dung left 3000-8000 years ago remains, at least partly frozen in ice (Gill 2012). Mosses are able to derive nutrients from these deposits, giving them much needed resources that are so scarce in the sand and gravel substrate of Antarctica.

Penguin rookeries on King George Island in the maritime Antarctic are an important source of nutrients and have a strong influence on the vegetation patterns and diversity (Smykla *et al.* 2007). The nutrient input, as guano, creates a zonation pattern. The first zone includes those areas under the immediate influence of fresh guano and trampling, supporting little or no vegetation. The second zone is adjacent to the first and is covered with nitrogen-loving green algae and sometimes Cyanobacteria. The third zone is dominated by Antarctic hair-grass. The fourth zone is dominated by mosses. The fifth and last zone under the rookery influence is dominated by lichens.

Peatland Habitats

Brewer (1967) pointed out that studies on bog vegetation were much more numerous than those on the animal populations. To help remedy this situation, he studied the breeding bird populations on two peatlands in lower Michigan. In the years 1961-1966 he noted 24 species of breeding birds in Portage Bog. These included the Song Sparrow (***Melospiza melodia***; Figure 40), Field Sparrow (***Spizella pusilla***; Figure 41), Yellowthroat (***Geothlypis trichas***; Figure 42), Yellow Warbler (***Setophaga petechia***; Figure 43), Nashville Warbler (***Leiothlypis ruficapilla***; Figure 44), Eastern Towhee

(***Pipilo erythrophthalmus***; Figure 45), Brown-headed Cowbird (***Molothrus ater***; Figure 46), Catbird (***Dumetella carolinensis***; Figure 47), American Goldfinch (***Carduelis tristis***; Figure 48), Traill's Flycatcher (***Empidonax traillii***; Figure 49), Black-capped Chickadee (***Poecile atricapillus***; Figure 50), Mourning Dove (***Zenaida macroura***; Figure 51), Cedar Waxwing (***Bombycilla cedrorum***; Figure 52), Yellow-shafted Flicker (***Colaptes auratus***; Figure 53), Cardinal (***Cardinalis cardinalis***; Figure 54), Brown Thrasher (***Toxostoma rufum***; Figure 55), Ruby-throated Hummingbird (***Archilochus colubris***; Figure 56), Mallard (***Anas platyrhynchos***; Figure 57), Marsh Hawk (***Circus cyaneus***), Eastern Bluebird (***Sialia sialis***; Figure 58), Tree Swallow (***Tachycineta bicolor***; Figure 59), Robin (***Turdus migratorius***; Figure 60), Whip-poor-will (***Caprimulgus vociferus***; Figure 61), and Veery (***Catharus fuscescens***; Figure 62). Among these, the Mallards were the only species for which the researchers located a nest, and the nest occurred in three of the six years. About 425 pairs were located there per hectare. Brown-headed Cowbirds were the most dense and Song Sparrows were the most abundant, the latter having an average of 138 territorial males per hectare. Others with a density of more than 24 per hectare were Yellowthroats, Field Sparrows, Eastern Towhees, and, perhaps, Brown-headed Cowbirds.

Figure 40. ***Melospiza melodia***, Song Sparrow, a species that commonly occurs in bogs during breeding season. Photo by Len Blumin, through Creative Commons.

Figure 41. ***Spizella pusilla***, Field Sparrow, a species that commonly occurs in bogs during breeding season. Photo by Jeff Whitlock, through Creative Commons.

Figure 42. ***Geothlypis trichas***, Yellowthroat, a species that commonly occurs in bogs during breeding season. Photo by Dan Pancamo, through Creative Commons.

Figure 43. ***Setophaga petechia***, Yellow Warbler, a species that commonly occurs in bogs during breeding season. Photo by Dick Daniels, through Creative Commons.

Figure 44. ***Leiothlypis ruficapilla***, Nashville Warbler, a species that commonly occurs in bogs during breeding season. Photo by Jerry Oldeneffel, through Creative Commons.

Figure 45. ***Pipilo erythrophthalmus***, Eastern Towhee, a species that commonly occurs in bogs during breeding season. Photo by Ken Thomas, through Creative Commons.

Figure 46. ***Molothrus ater***, Brown-headed Cowbird, a species that commonly occurs in bogs during breeding season. Photo through Creative Commons.

Figure 47. ***Dumetella carolinensis***, Grey Catbird, a species that commonly occurs in bogs during breeding season. Photo by Steve, through Creative Commons.

Figure 48. ***Carduelis tristis***, American Goldfinch, a species that commonly occurs in bogs during breeding season. Photo by MDF, through Creative Commons.

Figure 49. ***Empidonax traillii***, Willow Flycatcher, a species that commonly occurs in bogs during breeding season. Photo by Dominic Sherony, through Creative Commons.

Figure 50. ***Poecile atricapillus***, Black-capped Chickadee, a species that commonly occurs in bogs during breeding season. Photo by Zac Cota, through Creative Commons.

Figure 51. ***Zenaida macroura***, Mourning Dove, a species that commonly occurs in bogs during breeding season. Photo by R. L. Sivaprasad, through Creative Commons.

Figure 52. ***Bombycilla cedrorum***, Cedar Waxwing, a species that commonly occurs in bogs during breeding season. Photo by Cephas, through Creative Commons.

Figure 53. ***Colaptes auratus***, Yellow-shafted Flicker, a species that commonly occurs in bogs during breeding season. Photo by Minette Layne through Creative Commons.

Figure 54. ***Cardinalis cardinalis***, Cardinal in snow in Pickerington, OH, USA, a species that commonly occurs in bogs during breeding season. Photo courtesy of Eileen Dumire.

Figure 55. ***Toxostoma rufum***, Brown Thrasher, a species that commonly occurs in bogs during breeding season. Photo by E. Monk, through Creative Commons.

Figure 56. ***Archilochus colubris***, Ruby-throated Hummingbird, a species that commonly occurs in bogs during breeding season. Photo by Dan Pancamo, through Creative Commons.

Figure 57. ***Anas platyrhynchos*** female (left) and male (right), a species that commonly breeds and nests in bogs. Photo by Richard Bartz through Wikimedia Commons.

Figure 58. ***Sialia sialis***, Bluebird male, a species that commonly breeds in bogs. Photo from Sandy's Photos 2009, through Creative Commons.

Figure 59. ***Tachycineta bicolor***, Tree Swallow, a species that commonly occurs in bogs during breeding season. Photo by John Benson, through Creative Commons.

Figure 60. ***Turdus migratorius***, Robin, a species that commonly occurs in bogs during breeding season. Photo by Dakota Lynch, through Creative Commons.

Figure 61. ***Caprimulgus vociferus***, Whip-poor-will, a species that commonly occurs in bogs during breeding season. Photo by Jerry Oldeneffel, through Creative Commons.

Figure 62. ***Catharus fuscescens***, Veery, a species that commonly occurs in bogs during breeding season. Photo by Dominic Sherony, through Creative Commons.

In bogs studied by Brewer (1967), as the high thicket gave way to low thicket, some of the bird species changed, including the arrival of the Nashville Warbler (***Leiothlypis ruficapilla***; Figure 44) in 1965. The trees in the bog were not suitable for cavity-nesting birds during the study. Among these birds, Field Sparrows (***Spizella pusilla***; Figure 41) preferred open bog and Song Sparrows

(***Melospiza melodia***; Figure 40) preferred thickets, as did the Towhee (***Pipilo erythrophthalmus***; Figure 45), Yellowthroat (***Geothlypis trichas***; Figure 42), and Catbird (***Dumetella carolinensis***; Figure 47). The number of species in the open bog was about 13, whereas in the thicket it was about 21. When examining peatlands on a larger scale, Niemi and Hanowski (1992) found 110 species of birds that frequented Minnesota peatlands.

Brewer (1967) concluded that most of the birds came to the bog only for feeding. For example, Robins (***Turdus migratorius***; Figure 60) nested in the deciduous areas but came to the bog for feeding. This was especially true when berries were ripe, with both juveniles and adults coming to feed. Based on these habitat relationships, it is not surprising that most of the species in this bog were forest edge species. Brewer also considered it likely that some of the visitors, like the Meadowlark (***Sturnella magna***; Figure 63), mistook the open bog for an open field.

Figure 63. ***Sturnella magna***, Eastern Meadowlark, a bird that may occasionally mistake an open bog or fen for an open field. Photo by Jim F. Bleak, through Creative Commons.

Brewer (1967) only observed birds in the Sugarloaf Bog for two years. This site had 26 breeding bird species during that time, with the average per year of about 20 species. The density was high, with about 675 males per hectare. The **Black-capped Chickadee** (***Poecile atricapillus***; Figure 50) was the most abundant, with about 100 males per hectare (compared to 10 at Portage Bog).

Only nine species were common to both locations (Brewer 1967). In a larger study based on literature, Brewer found that there is little commonality among species of the open bog. Birds of the spruce forest, on the other hand, are similar to those of a cedar forest or a spruce thicket. It became clear that species of the bogs depended on the vegetation of that stand and on the vegetation of adjacent areas, as well as the geographic distribution of the species. Few birds were present in the winter, reflecting the poor winter food supply and insufficient cover.

Calmé and Desrochers (1999, 2000) and Calmé *et al*. (2002) investigated the birds in 67 southern Quebec, Canada, peatlands. They expressed concern over the loss of peatlands to urban sprawl, agriculture, forestry, and peat mining, particularly in eastern Canada (Calmé & Desrochers 2000). This loss further fragments the peatlands, making natural re-introductions more difficult. This isolation causes the peatlands and their bird populations to behave with island dynamics. Among ten species of birds studied in detail, two rely primarily on peatlands for nesting sites. Bird species richness was primarily related to microhabitat richness and heterogeneity. The Palm Warbler (***Dendroica palmarum***; Figure 64) and Upland Sandpipers (***Bartramia longicauda***; Figure 65) depended on having larger, non-isolated peatlands.

Figure 64. ***Dendroica palmarum***, Palm Warbler, a species that depends on large, non-isolated peatlands. Photo by Wolfgang Wander, through Creative Commons.

Figure 65. ***Bartramia longicauda***, Upland Sandpiper, a species that depends on large, non-isolated peatlands. Photo by Johnath, through Creative Commons.

Calmé *et al*. (2002) found 17 species of birds that were significantly more frequent in peatlands than in the surrounding habitats. For some, the peatland was one of several habitats, but some were significantly more frequent in peatlands.

In studying 28 southeastern Quebec, Canada, peatlands, Desrochers *et al*. (1998) found that harvesting

effects on birds depended on the type of harvesting. Block harvesting had the least effect, presumably because it retained most of the topography and microhabitats. Vacuum harvesting, on the other hand, did alter the bird communities. Ten of the 28 species responded negatively to peatland perturbation. The Palm Warbler (***Dendroica palmarum***; Figure 64), in particular, was closely associated with the unperturbed sites.

The Palm Warbler (***Dendroica palmarum***; Figure 64) is an area-sensitive bird and in southern Québec it is restricted to peatlands (Poulin 2002). The within-site habitat configuration strongly affects the physical efficiency of this species but not necessarily functional effectiveness. While it is clear that having a number of peatlands available is important to the Palm Warbler, the biological factors they provide remain elusive.

When Lachance *et al.* (2005) investigated 16 peatlands in southern Quebec, Canada, they found 36 bird species and 154 plant species. They found that afforestation altered the vegetation structure in ways that changed the bird species composition. In particular, there were fewer mosses and shrubs, but more trees.

One reason for the diminished number of birds in disturbed peatlands is the loss of eggs and nestlings to predation. Haddad *et al*. (2000) assessed the effects of harvesting peat mosses on the survival of bog-dwelling songbirds [Palm Warbler (***Dendroica palmarum***; Figure 64), Common Yellowthroat (***Geothlypis trichas***; Figure 42), Hermit Thrush (***Catharus guttatus***; Figure 66), and several species of sparrows (**Passeridae**; Figure 40-Figure 41)]. They found greater risk of nest predation in harvested bogs.

Figure 66. ***Catharus guttatus***, Hermit Thrush, a species that loses more eggs to predation in harvested bogs than in undisturbed bogs. Photo by Cephas, through Creative Commons.

Another possibility to explain loss of birds on harvested peatlands is disruption of the habitat of food organisms. **Diptera** larvae, especially the cranefly ***Tipula*** (Figure 67), live and pupate among the mosses in the peatland (MacLean 1980). The birds consume 35-70% of annual production of ***Tipula carinifrons*** and consume 50% of adults at peak emergence. The cranefly larvae feed on liverworts in these bogs (Coulson & Whittaker 1978). Paasivirta *et al*. (1988) likewise noted the importance of emerging insects for feeding birds in peatlands.

Figure 67. ***Tipula***, leatherjacket larva, a genus that is eaten in great numbers by birds in bogs. Photo by Rasbak, through Creative Commons.

Effects on Bryophyte Community Structure

Birds can have considerable influence on bryophyte communities, especially in Arctic wetlands. We have already seen that guano from seabirds can provide nutrients that are otherwise limiting. And Pheasants (Figure 68) can disrupt the community while searching for food (Erkamo 1976).

Figure 68. ***Phasianus colchicus***, Pheasant, a forager that can disturb bryophytes while foraging. Photo by Hugh J. Griffiths, through Creative Commons.

In the Arctic, **geese** (Figure 69) can play a role in community structure (Jasmin *et al*. 2008). Although one might expect such feeding disruption to reduce the number of species, Jasmin and coworkers found greater bryophyte species richness following 11 years of goose presence, compared to that in goose exclosures. The non-protected areas exhibited more variation in time and space than within the exclosures, promoting greater coexistence of bryophyte species at the microscale of 1 cm.

Figure 69. ***Chen caerulescens***, migratory Snow Geese, foraging. Photo by Bradley Davis, through Creative Commons.

Conservation Issues

Agricultural areas might actually help bird species diversity in tropical forests (Hughes *et al.* 2002; Sekercioglu *et al*. 2007). Although we typically think of deforestation for agriculture as being detrimental to bird diversity, researchers found that most of the 144 bird species used the agricultural areas for foraging, often travelling several kilometers from their forest home (Hughes *et al.* 2002). They estimated that 46% of the native birds were using the agricultural countryside in southern Costa Rica. The authors suggest that diversity will suffer less if tall trees and edge habitats are maintained.

In an effort to understand how to protect birds with minimal effort, we have often chosen indictor species (Simberloff 1998). Unfortunately, these are not as indicative as we might hope. It is difficult to know what species should be the indicator and on just what it should indicate. Simberloff suggested instead that the species should be an "umbrella species,... one that needs such large tracts of habitat that saving it will automatically save many other species."

A flagship species is typically a charismatic large vertebrate, such as the panda or a snowy owl (Anonymous, USDA; Simberloff 1998). It is useful because it causes both public interest and sympathy (Simberloff 1998). It suffers some of the same problems – it may not be in an area that protects many other species, and it might be expensive to protect. And management of one flagship species may conflict with that of managing another. "The recognition that some ecosystems have keystone species whose activities govern the well-being of many other species suggests an approach that may unite the best features of single-species and ecosystem management. If we can identify keystone species and the mechanisms that cause them to have such wide-ranging impacts, we would almost certainly derive information on the functioning of the entire ecosystem that would be useful in its management."

Even keystone species can get complicated. As seen in a Colorado subalpine ecosystem, there may be subtle interdependencies (Daily *et al.* 1993). The Red-naped Sapsuckers (***Sphyrapicus nuchalis***; Figure 70) actually have two keystone roles. Their excavation activities to make nests in fungus-infected aspens are essential to two species of swallows, and when they drill sap wells into willows they nourish not only themselves, but also make this rich food source available to Hummingbirds (Figure 56), Orange-crowned Warblers (***Vermivora celata***; Figure 71), chipmunks (***Tamias striatus***), and other sap robbers. Thus for this community to persist, it requires the complex interactions of sapsuckers, willows, aspens, and a heartwood fungus.

As an example, the penguin (Figure 39) can be a keystone species in the maritime Antarctic (Barcikowski *et al*. 2005). We have seen above that the guano produced by the penguins can form the base for an entire community by providing an important supplement to the rare nutrients. In areas where the guano enriches the substrate with nutrients originating in the ocean, the grasses *Colobanthus quitensis* (Figure 72) and *Deschampsia antarctica* (Figure 73) predominate. Where the guano is absent, mosses such as ***Polytrichum piliferum*** (Figure 74) predominate.

Figure 70. ***Sphyrapicus nuchalis***, Red-naped Sapsucker, a keystone bird species. Photo by Dominic Sherony, through Creative Commons.

Figure 71. ***Vermivora celata***, Orange-crowned Warbler, a species that depends on the Red-naped Sapsucker as a keystone species. Photo by Linda Tanner, through Creative Commons.

Figure 72. ***Colobanthus quitensis***, a dominant Antarctic species in areas enriched by guano. Photo by John Clark, through Creative Commons.

Figure 73. ***Deschampsia antarctica***, a dominant Antarctic species in areas enriched by guano. Photo by John Clark, through Creative Commons.

Figure 74. ***Polytrichum piliferum***, a moss that avoids areas with guano in the maritime Antarctic. Photo by Bob Klips, with permission.

To put this in a bryological perspective, we may find that a species is dependent on mosses in spring before herbaceous plants are available or in winter when tracheophytes cease growing. The bryophytes might depend on one or more species of birds for the bulk of their dispersal. Or the bryophytes might serve as emergency foods during years when the weather is not suitable for good productivity of other, more preferred foods. With so many possibilities, we have just begun to understand the interrelationships.

Dispersal Agents

If you have ever reared Zebra Finches (***Taeniopygia guttata***; Figure 75), you know that they are incessant nest-builders. It was impossible to keep mosses in my garden room when I had finches because these mosses were prime nest-building material. But as you would also observe, not all selected mosses made it to the nest. Pieces would fall as the birds flew, and even the nest itself would occasionally lose pieces, but fragments would especially get dropped beneath the nest as the building progressed, in some cases deliberately as the birds determined that piece to be too recalcitrant to become part of the architecture.

In addition to fragments and propagules travelling among feathers, it is also possible for bryophyte parts to travel in the digestive system of birds (Behling *et al*. 2016). On Navarino Island, at the Cape Horn Biosphere Reserve, these researchers recovered bryophyte diaspores from fecal samples from the Upland Goose (***Chloephaga picata***; Figure 34) and the White-bellied Seedsnipe (***Attagis malouinus***). Viability remains to be established.

Figure 75. ***Taeniopygia guttata***, Zebra Finch, a pet that is an incessant nest builder and uses mosses, among other things. Photo from Sky High Butterfly, through Creative Commons.

Davison (1976) describes the role of birds in the dispersal of mosses. Indeed, it was not the nest-building activities, but feeding activities that caught his attention. Where leaf litter is somewhat scarce, such as older beech woods, and mosses are abundant, foraging requires that the birds poke around among the mosses. **Blackbirds** (***Turdus merula***, Figure 76) in particular foraged among ***Mnium hornum*** (Figure 25) and ***Polytrichastrum formosum*** (Figure 77), breaking the plants and scattering them much like the Japanese do when planting a moss garden. Davison reports that within a two-month period these birds moved 34 clumps of moss from one place to another within an area of about 5 m^2, but also brought to the area an additional 18 pieces.

Figure 76. ***Turdus merula*** (Blackbird), a species that forages among ***Mnium hornum*** and ***Polytrichastrum formosum***. Photo by Mario Modesto Mata through GNU Free Documentation.

Figure 77. ***Polytrichastrum formosum***, a moss where Blackbirds forage, disturbing the moss. Photo by David T. Holyoak, with permission.

But it appears that might not be the only reason to cause **Blackbirds** (***Turdus merula***; Figure 76) to scatter bryophytes. Robin Stevenson reports (Bryonet 25 April 2010) observing a male of this same species of bird throwing clumps of mosses off a roof, alternately with mid air attacks by another Blackbird – a classic example of displacement! There was too much activity to discern if both birds were moss throwers. Apparently the two were fighting over territory or some other disagreement and the mosses were handy objects to throw from their rooftop habitat. In this case, the lucky roof mosses were ***Grimmia pulvinata*** (Figure 78), ***Hypnum cupressiforme*** (Figure 79), and ***Syntrichia montana*** (Figure 80). When on the ground they threw cockle shells and other things.

Figure 78. ***Grimmia pulvinata***, a moss thrown about by a Blackbird during a territorial competition. Photo by Michael Lüth, with permission.

In another instance, Davison (1976) found spores of a moss on the feet of a dead Song Thrush (***Turdus philomelos***; Figure 81). Although most of the scavenging activity probably only transports moss fragments and spores for short distances, spores might occasionally be transported by feet, feathers, and beaks to considerable distances following such activity.

Figure 79. ***Hypnum cupressiforme***, a species thrown about by Blackbirds in displacement activity. Photo by Jan-Peter Frahm, with permission.

Figure 80. ***Syntrichia montana*** (Intermediate Screw-moss), a species thrown about by Blackbirds in displacement activity. Photo by Barry Stewart, with permission.

Figure 81. ***Turdus philomelos***, Song Thrush, a bird known to carry mosses on its feet. Photo by Brian Eversham, with permission

But birds are imperfect in their industrious movement of moss from natural substrate to nest. Bits fall, and hence alight in a new location. This facilitated dispersal, while

somewhat random, can be quite helpful in moving rarely fruiting mosses about. Chmielewski and Eppley (2019) found that when birds use bryophyte-covered areas for foraging and gathering nesting material, they can acquire propagules on their legs, feet, and tails. The researchers successfully germinated propagules from among the 242 propagules and 1512 spores they collected from 224 birds, comprised of bird 34 species. They found the tail feathers to be the greatest dispersal agents among bark and foliage species. Hence, birds are potential dispersal agents.

The Pintail Duck (***Anas acuta***; Figure 82) is a likely agent of dispersal of ***Riccia rhenana*** (Figure 83) (McGregor 1961). In this liverwort, the older parts die, but the apices survive two months of drought and five weeks submersion in ice, making it likely that they would survive transport among the feathers of the Pintail Duck.

Figure 82. ***Anas acuta***, Northern Pintail male and female, agents of aquatic bryophyte dispersal, especially ***Riccia rhenana***. Photo by J. M. Garg, through Creative Commons.

Figure 83. ***Riccia rhenana***, a species dispersed by pintail ducks. Photo by Štěpán Koval, with permission.

Lewis *et al*. (2014b) suggested that ***Tetraplodon*** (Figure 84) species were distributed long-distances by birds. They reasoned that the absence of wind patterns to account for their distribution in the New World and the sensitivity of the spores to extreme environmental conditions, bird dispersal, probably on feathers, was the most reasonable explanation. In support of this possibility, Lewis *et al*. (2014a) demonstrated bryophyte diaspores among the feathers of transequatorial migrant birds.

Figure 84. ***Tetraplodon mnioides*** with mature capsules; this species may be distributed by birds. Photo by Richard Caners, with permission.

Des Callaghan filmed a site where the White Wagtail (***Motacilla alba***; Figure 85) frequently perches on a particular branch. That branch is covered by ***Splachnum vasculosum*** (Figure 86-Figure 87). Does the bird simply like the soft moss and its location? Is the moss dispersed by the feathers and feet of the birds? Or might it be deposited in feces, indicating the birds ate the capsules?

Figure 85. ***Motacilla alba alba***, White Wagtail, a species that spends much time on a branch with ***Splachnum vasculosum*** in Wales. Photo by Luis Garcia, through Creative Commons.

Figure 86. ***Splachnum vasculosum*** growing on a branch next to a stream and the site where the White Wagtail, ***Motacilla alba***, prefers to perch. Photo courtesy of Des Callaghan.

Figure 87. ***Splachnum vasculosum*** capsules. Photo by Dick Haaksma, with permission.

In some way the petrels and other sea birds seem to be responsible for the locations of members of **Calymperaceae** in the Chathams and other areas around New Zealand. Fife and Lange (2009) suggest dispersal by birds. They consider it likely that the sea birds may have contributed to dispersal of the moss ***Calymperes tenerum*** (Figure 88) on the Chatham Islands and the Kermadecs to the north and east of New Zealand, respectively. Peter de Lange (pers. comm. 12 June 2017) reported that until 80-100 years ago, Tube Nose Petrels, especially ***Pterodroma*** spp. (Figure 92-Figure 93), were influential, but Broad-billed Prions (***Pachyptila vittata***) and shearwaters (***Puffinus griseus***; Figure 89) also were common in the areas where ***Calymperes*** grows now, but that these birds disappeared 80-100 years ago.

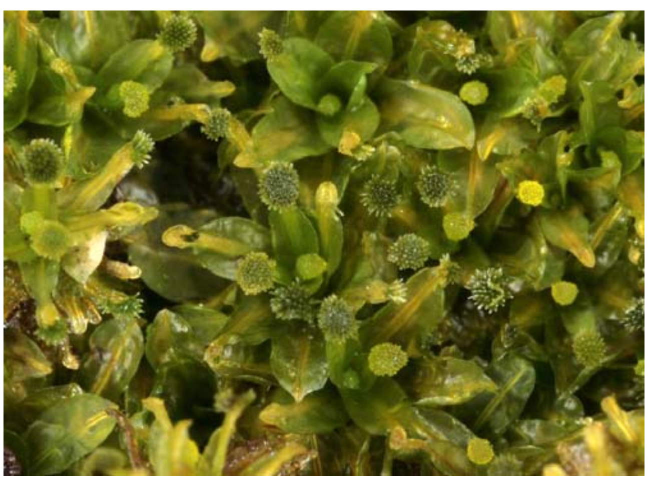

Figure 88. ***Calymperes tenerum***, a species that may have been dispersed long distance by the Shearwater. Photo by Jan-Peter Frahm, with permission.

Later, de Lange (Peter de Lange, pers. comm. 12 June 2017) found ***Syrrhopodon armatus*** (Figure 90-Figure 91) on the smallest of the main Chatham Island, Rangatira. This island is free of predators and supports a million plus seabirds. The ***S. armatus*** grows on tree trunks that are used by the petrels and Broad-billed Prions (***Pachyptila vittata***) as runways. They also grow around the burrows of these birds, especially those of the Chatham Petrel (***Pterodroma axillaris***). On Rabbit Island, ***Syrrhopodon*** grows around the active burrows of shearwaters (***Puffinus griseus***; Figure 89) and diving petrels.

Figure 89. ***Puffinus griseus***, Sooty Shearwater, a possible dispersal agent for ***Calymperes tenerum*** (Figure 88). Photo from USGS photograph by Jonathan Felis, through public domain.

Figure 90. ***Syrrhopodon***, a genus that might be dispersed by sea birds in islands around New Zealand. Photo by Jan-Peter Frahm, with permission.

Figure 91. ***Syrrhopodon armatus*** leaf, a possible propagule carried by sea birds to islands around New Zealand. Photo from Natural History Museum, London, through Creative Commons.

In addition to these islands, on the Chatham island of Rekohu and the Pitt island of Rangiuria, ***Calymperes*** (Figure 88) is found only in locations there the

pterodromids once had dense nesting locations, as indicated by remains of their burrows (Peter de Lange, pers. comm. 12 June 2017). At the location where de Lange first found ***C. tenerum*** (Figure 88) there are still seabirds, including Taiko (***Pterodroma magentae***), a critically endangered species (Fife 2009).

In New Zealand at Te Paki, ***Calymperes*** (Figure 88) again is associated with ***Pterodroma nigripennis*** (Figure 92) and ***P. gouldi*** (Peter de Lange, pers. comm. 12 June 2017). And on Raoul Island, all the locations found by de Lange were also in areas frequented by the Kermadec Petrel (***Pterodroma neglecta neglecta***; Figure 93) until the rats wiped them out early in the 20th Century. As on the Chatham Islands, the birds used the trees with ***Calymperes*** (Figure 88) as runways.

Figure 92. ***Pterodroma nigripennis***, a species that seems to be associated with ***Calymperes*** (Figure 88) and may disperse it. Photo by Christopher Watson, through Creative Commons.

Figure 93. ***Pterodroma neglecta***, Kermadec Petrel, a species always found with ***Calymperes*** on Raoul Island. Photo by Lance Andrewes, through Creative Commons.

On the Poor Knights Islands, Jessica Beever has similarly collected ***Syrrhopodon armatus*** (Figure 90-Figure 91) associated with a heavily burrowed petrel area (Allan Fife, pers. comm. 12 June 2017).

Based on what we know about these seabird-**Calymperaceae** relationships there are three plausible explanations for the relationships. The birds may fertilize the bark with guano, thus providing nitrogen for the mosses. The birds may serve as dispersal agents. The mosses may provide foraging substrate for the birds. Felicisimo *et al*. (2008) provided evidence that the Cory's Shearwater (***Calonectris diomedea***; Figure 94) follows wind patterns that could explain dispersal patterns. Cameron *et al*. (2006) have suggested that Buller's Shearwater (***Puffinus bulleri***; Figure 95) best explains the presence of the fern *Asplenium pauperequitum* on the Chatham Islands group, a distance of 1245 km from its nearest neighbor. This bird is a New Zealand endemic species and has large breeding populations on the Poor Knights Islands where *Asplenium pauperequitum* was originally described (Allan Fife, pers comm. 12 June 2017). In the Chathams it does not breed, but it is a regular visitor. Any and all of these explanations for the **Calymperaceae**-seabird associations may be true.

Figure 94. ***Calonectris diomedea***, Cory's Shearwater flying, permitting it to disperse bryophytes over long distances. Photo by A. H. Kopelman, through Creative Commons.

Figure 95. ***Puffinus bulleri***, Buller's Shearwater, a species that might disperse mosses to islands near New Zealand. Photo by Tom Tarrant, through Creative Commons.

Chmielewski (2015) sought to support these suggestions by culturing propagules found on birds caught with mist nets. Using cotton swabs, he sampled feet, legs, and flight feathers. The spores obtained were cultured on nutrient agar. The resulting bryophyte plants were identified by PCR amplification and Sanger sequencing of the trnL region of the chloroplast genome. We shall have

to look forward to the revelation of these species when this work is published.

Dispersal of bryophytes by birds is discussed in more detail in subchapters 4-9 and 4-11 of Volume 1.

Soft Landings

Pole jumpers have sand pits or mats to protect them when they land. To me it seems reasonable that birds might choose soft landing sites as well. Birds in captivity often get a condition known as **bumblefoot** (Figure 96) (Halliwell 1975; Hawkey *et al*. 1985), but the condition can occur in wild populations, albeit much less commonly (Gentz 1996). Bumblefoot can be caused by rough perches, sandpaper on the perch, sharp corners, dirty perches, or all perches of the same size. In the wild these problems are largely absent, explaining the scarcity of bumblefoot in nature. Do wild birds select landing spots on the basis of the presence of the spongy bryophytes and lichens (Figure 97)?

Figure 96. Eagle bumblefoot, a common condition for birds of prey in captivity. Photo by Richard Jakowski, through Creative Commons.

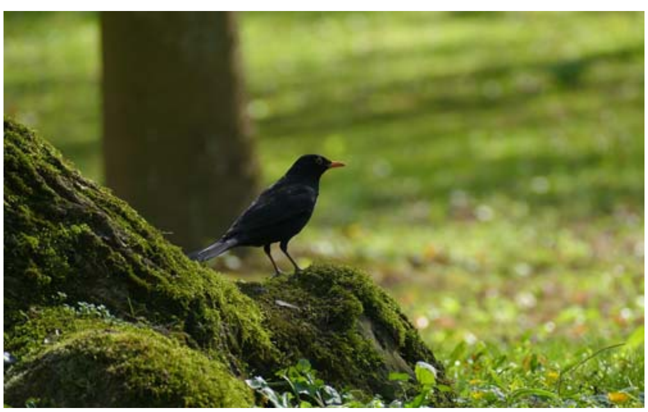

Figure 97. Bird on moss perch – Is it a sentinel, or just cooling its feet on the moss? Photo by Ervin Gjata, through public domain.

Summary

Birds interact with bryophytes by foraging among them, eating them, eating capsules, getting a drink, building nests or parts of nests with them, using them as breeding grounds, using moss hummocks as **watch towers**, throwing them in displacement behavior, bathing among them, and getting dry on them. On the other hand, the birds may help the bryophytes as dispersal agents and by providing fertilizer as guano. Or they may seriously disturb them during their foraging. Others provide so much guano that the bryophytes are intolerant of it. Soft bryophytes might also help to prevent bumblefoot in wild birds.

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CHAPTER 16-2
BIRDS AND BRYOPHYTIC FOOD SOURCES

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CHAPTER 16-2 BIRDS AND BRYOPHYTIC FOOD SOURCES

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.

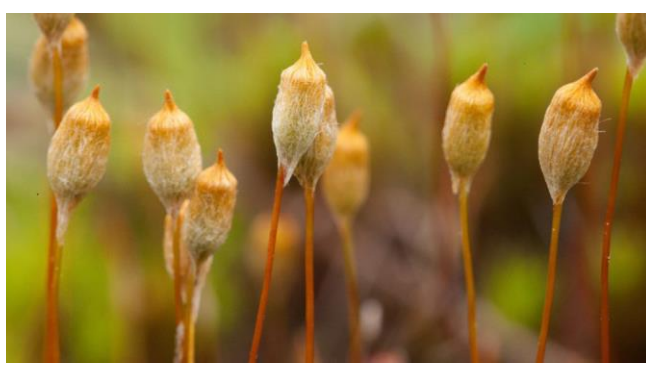

Figure 2. ***Polytrichum commune*** capsules, food for White-throated Sparrows (***Zonotrichia albicollis***) and Norwegian Grouse (***Tetrao urogallus***?) chicks. Photo by Bob Klips, with permission.

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

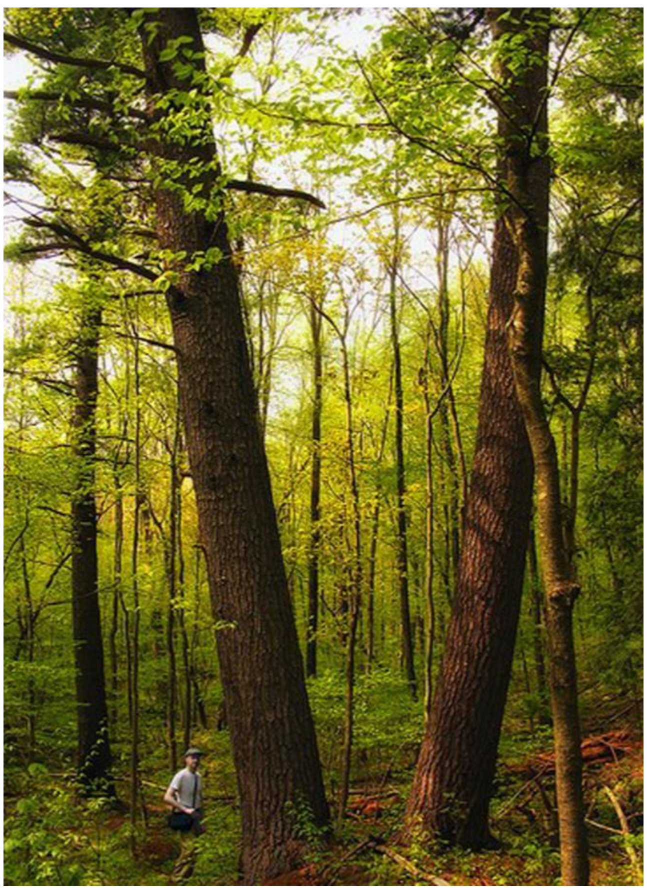

Figure 4. ***Pinus strobus*** (white pine) forest, Pennsylvania. Photo by Nicholas T., through Creative Commons.

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.

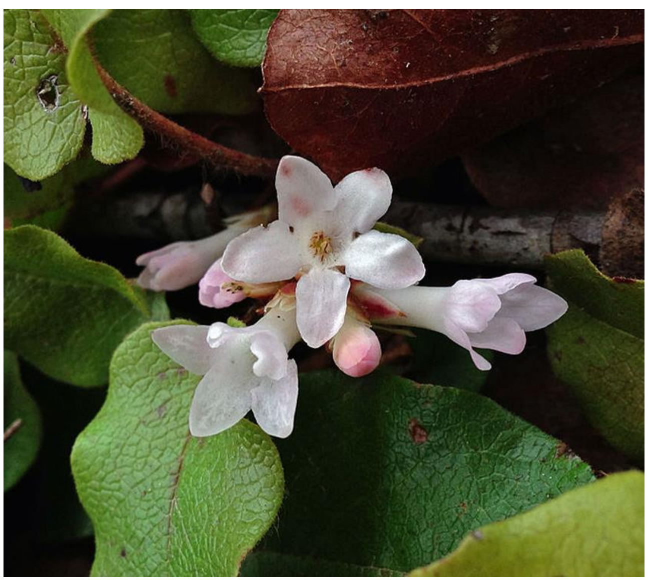

Figure 25. ***Epigaea repens***, one of the two most preferred foods of grouse chicks. Photo by Fritz Flohr Reynolds, through Creative Commons.

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.

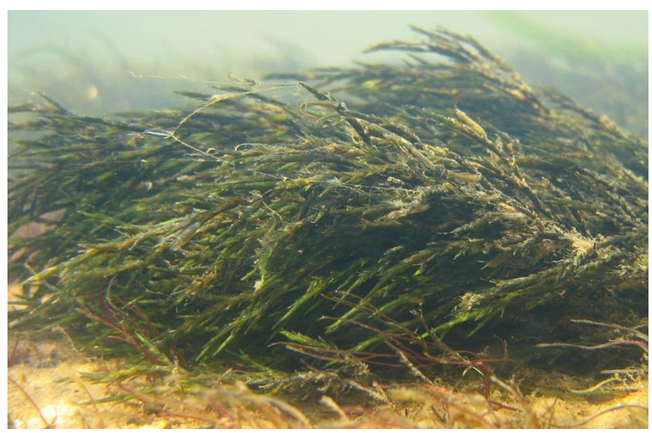

Figure 49. ***Fontinalis novae-angliae*** protecting invertebrates from Canada Goose grazing because the geese won't eat it. Photo by John Parker, with permission.

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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CHAPTER 16-3
BIRD NESTS

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BIRD NESTS

Figure 1. Nest with mosses, lichens, and baby birds. Photo by Kytka through public domain.

Nests

Within a thick and spreading hawthorn bush
That overhung a molehill large and round,
I heard from morn to morn a merr thrush
Sing hymns of rapture, while I drank the
Sound with joy – and oft an unintruding guest,
I watched her secret toils from day to day;
How true she warped the moss to form her nest,
and modell'd it within with wood and clay.

The Thrush's Nest, by Claire
(in Marshall 1908)

Nests are complex structures that often consist of structural differences within a single nest. Most bird nests occur in unique habitats and are constructed of specific materials (Heinrich 2000). The nests themselves are typically so unique that the owner/builder can be identified by the nest. In some cases, false nests are built by the male to discourage would-be suitors from enticing the female away.

The greatest vulnerability in the life cycle is typically during the time the young birds are in the nest (Heinrich 2000). Thus the construction and location of the nest are important survival factors (Heinrich 2000; Mainwaring *et al*. 2012). Most nests are built by the females, but in some cases it is the male who builds the nest(s), using them as sex attractants (Heinrich 2000). But the female typically chooses the site.

Although many nests are built for one-time use by the builder, some nests are reused by the same bird or by other animals for other purposes (Heinrich 2000). For example, the deermouse climbs the tree to find a bird nest, then relocates it near the ground and fills it with seeds to store for the winter.

The importance of bryophytes in the Antarctic is illustrated at Vestfold Hills, East Antarctica. There was greater species diversity of mosses and lichens in sites

adjacent to nests than away from them. Is this a **guano** (bird droppings) benefit to the bryophytes, a moisture or insulation benefit to the birds, or a combination of both? Or do the bryophytes simply like the same locations as the birds? Soil nutrients were not significantly associated with moss diversity or abundance. Rather, both species and abundance of mosses have a positive association with soil water content. So it may be that the birds prefer nesting sites that are also preferred by the mosses.

Types of Nests

Wikipedia (2017) defines nine types of nests. The most common and familiar of these is the **cup** nest that is the product of many of the passerine birds.

The **scrape** nest (Figure 2) is the simplest. It is merely a depression in the soil or vegetation, but it may benefit from the addition of materials, such as bits of vegetation, small stones, shell fragments, or feathers. Mosses may form the base of such a nest. It usually has a rim to prevent eggs from rolling away. This type of nest is the most exposed, thus offering the least protection. This nest style is used by ostriches, many kinds of ducks, most shorebirds, most terns, some falcons, pheasants, quail, partridges, bustards, and sand grouse.

Figure 2. The **scrape** nest of ***Charadrius*** sp., a plover. This nest is lined with shells to support the eggs when the soil or sand become muddy. Photo by Gniazdo Sieweczki RB, through Creative Commons.

The **mound** nest (Figure 3) is typically made of soil, branches, sticks, twigs, and/or leaves (Wikipedia 2017). The females lay their eggs within the mounds, and the rotting vegetable matter generates heat that helps to warm and incubate the eggs. The largest of these nests is that of the Australasian megapodes. In some cases, as in the Australian Brush Turkey (*Alectura lathami*), the gender of the hatched eggs is affected by the temperature, with more females at higher temperatures (Göth 2007). Others building mound nests include the horned coot and the flamingo (Wikipedia 2017).

Figure 3. Malleefowl **mound** nest. Photo by Glen Fergus, through Creative Commons.

The **burrow** is an underground excavation that may be created by the bird or repurposed from a previous mammalian or tortoise owner (Wikipedia 2017). These are sometimes lined with mosses and usually have a tunnel entrance to an egg chamber. The bird occupants include white-browed tits, puffins, shearwaters, some megapodes, motmots, todies, most kingfishers, the crab plover, miners, and leaftossers.

Figure 4. The Sand Martin, *Riparia riparia*, in **burrow** nest. Photo by Bruce, through Creative Commons.

The **cavity** nest (Figure 5) is built in living or dead wood, tree ferns, or some cacti (Wikipedia 2017). The **cavity** nester is more likely to use bryophytes than the above-named nest builders. These are used to line the cavity and to elevate the base to a suitable height for entering and feeding the young birds. Some of the birds excavate their own cavities (woodpeckers, trogons, some nuthatches, many barbets). But far more species (parrots, tits, bluebirds, most hornbills, some kingfishers, some owls, some ducks, some flycatchers) must find holes already large enough.

Figure 5. *Dryocopus martius* (Black Woodpecker) with its **cavity nest**. Photo by Alastair Rae, through Creative Commons.

When most people think of a bird nest, it is the **cup** nest (Figure 6) that they visualize. These nests are open from the top and smoothly hemispherical inside, with a deep depression to house the eggs (Wikipedia 2017). The materials used are mostly pliable and some species specifically use bryophytes, either in the construction, the lining, or the outermost layer – perhaps as camouflage. The nest mass often correlates with the weight/size of the adult bird it must support. The insulation quality of the nest relates to nest mass, nest wall thickness, nest depth, nest weave density and porosity, surface area, height above ground, and elevation above sea level. Among the many cup builders are the robin and the tiny hummingbird. Some are attached to the branch with saliva, and some hummingbirds use spider webs to affix the nest.

Figure 6. ***Passerculus sandwichensis***, Savannah Sparrow **cup** nest. Photo by Kati Fleming, through Creative Commons.

The **saucer** or **plate** nest is somewhat similar to the cup nest, but has very little, if any, depression (Wikipedia 2017). This nest may be within the range of nest variation for a cup builder.

The **platform** nest (Figure 7) is large and flat. It is occasionally lined with mosses (Wikipedia 2017). This nest type is common among some ducks and birds of prey. This more permanent structure can be used y the same pair of birds for many years.

Figure 7. Osprey (*Pandion haliaetus*) and **platform** nest. Photo by Tibor Duliskovich, through Creative Commons.

The **pendant** nest (Figure 8) is an elongated sac that hangs from a branch (Wikipedia 2017). Pendant nest builders include Oropendolas, caciques, orioles, weavers, and sunbirds. Some of these birds construct their nests from bryophytes.

Figure 8. ***Ploceus castaneiceps*** (Taveta Golden-weaver) **pendant** nest. Photo by Robert Lawton, through Creative Commons.

The **sphere** nest (Figure 9) is a globe-shaped nest that is completely enclosed except for a small opening which may be near the bottom (Wikipedia 2017).

Figure 9. Weaver (**Ploceidae**) on **sphere** nest. Photo by Bernard Dupont, through Creative Commons.

Bryophyte Advantages in Bird Nests

Use of mosses for bird nests is not uncommon. Annie Martin (Bryonet 1 June 2010) reports that as many as forty different types of birds use mosses in constructing their nests. While that may be a local number, many more examples are known worldwide. Birds have long been recognized as consumers of mosses and liverworts for nesting materials (Figure 10) (Takaki 1957, Breil & Moyle 1976 – SE USA; Takeshita 1978, Furuki & Onuma 1996 – Japan; Hribek 1985 – Europe; Abolina 1991 – Lithuania; Cao & Caihua 1991, Cao *et al*. 2010 – China), to name a few. Richardson (1981) listed 53 British birds that use mosses to some degree in their nests; Campbell and Ferguson-Lees (1972) reported 52 from that region. Jadin and Billiet (1979) described the activities of birds building nests with mosses and liverworts on Reunion Island in the Indian Ocean.

Figure 10. Cup nest made of leafy liverworts in Costa Rica. Photo courtesy of Dave Fenlon.

Birds and bryophytes can have close relationships that permit both of them to reproduce. Some birds have an incessant need to make nests, and mosses can be a favorite building material. I found it impossible to develop any kind of moss garden in my garden room when it housed 10 Zebra Finches (***Taeniopygia guttata***; Figure 11) because within days or even hours every scrap of the moss had been moved from my chosen location to the midst of the bamboo clump, where it aided in forming massive 3-story apartment nests. I ultimately had to get rid of the finches and traded them for Society Finches, birds that have a little more reverence for mosses and don't find nest building to be an essential daily activity!

Figure 11. ***Taeniopygia guttata***, Zebra Finch, a bird that often uses mosses in its nests, at least when choices are limited. Photo by Peripitus, through Creative Commons.

The families of birds using mosses to some degree in their nests ranges widely. We need consider only a few examples to illustrate this. In the **Passeriformes**, Hribek (1985) found that among others in the **Paridae**, the Great Tit (***Parus major***; Figure 18-Figure 19) and the Blue Tit (***Cyanistes caeruleus***; Figure 22) use mosses in their nests, as does the Pallas Dipper (***Cinclus pallasii***; Figure 12) in the **Cinclidae** (Nishimura *et al.* 1980). In the **Apodiformes: Apodidae**, the Philippine Swiftlet (***Aerodramus mearnsi***; Figure 13) uses bryophytes (Tan *et al*. 1982). In the **Podicipediformes: Podicipedidae**, breeding populations of the Red-necked Grebe (***Podiceps grisegena***; Figure 14-Figure 15) in the Northwest Territories use ***Sphagnum*** (Figure 16) in addition to cattails and other emergent vegetation in nest construction (Fournier & Hines 1998). Even the huge American Bald Eagle (***Haliaeetus leucocephalus*** in the **Falconiformes: Accipitridae**; Figure 17) in Alaska uses mosses in old-growth forests in their nests atop tall spruce trees (Holleman 1997).

Figure 12. ***Cinclus pallasii***, Brown dipper, Pallas Dipper, in stream. This species collects aquatic mosses to make its nest. Photo by Alpsdake, through Creative Commons.

Figure 13. ***Aerodramus mearnsi***, Philippine Swiftlet, with its challenging moss nest. Photo by Angie Cederlund, with permission.

Figure 14. ***Podiceps grisegena***, Red-necked Grebe with ducklings, a species that uses mosses in its nest. Photo through public domain.

Figure 15. ***Podiceps grisegena***, Red-necked Grebe, on its nest with nestlings on its back. Photo by Lukasz Lukasik, through Creative Commons.

Figure 16. ***Sphagnum fimbriatum***; ***Sphagnum*** is used as a nest material for the Red-necked Grebe. Photo by James K. Lindsey, with permission.

Figure 17. ***Haliaeetus leucocephalus***, American Bald Eagle landing on nest. This species uses mosses in building its nest in Alaska. Photo by Murray Foubister, through Creative Commons.

With such a large number of birds using bryophytes in their nests, we must ask why? Do they provide some special attributes that make them desirable? Or are they simply easy to collect and available?

Alabrudzińska *et al*. (2003) found that the quantity and proportion of mosses in nests and the nest size can influence the success of eggs as well as of the nestlings, as seen in the Great Tits (***Parus major***; Figure 18-Figure 19). They considered that nest size and composition must satisfy contradictory pressures needed for survival. The nest must be kept moist with a relatively constant temperature. It must also protect the eggs and young from predation and limit disease and parasites.

Figure 18. ***Parus major***, Great Tit male, a bird that includes mosses in its nest. Photo by Charles J. Sharp, through Creative Commons.

Figure 19. ***Parus major*** nest with moss, down, and nestlings. Photo by Notts Ex Miner, through Creative Commons.

Insulation

Bryophytes can have beneficial effects that are not provided by other nesting materials. Providing insulation may be the first use that comes to mind. Birds often use grasses, feathers, and fur to regulate the nest temperature (Bartholomew *et al.* 1976; Winkler 1993; Blem & Blem 1994; Lombardo *et al.* 1995), much as we put on a winter coat or sleep under a quilt. But bryophytes can provide insulation as well.

Several studies have indicated the importance of nest temperature. Olson *et al.* (2006) used Zebra Finches (***Taeniopygia guttata***; Figure 11) to evaluate the importance of temperature on embryo development. They found that after 12 days of incubation, periodic cooling resulted in lower embryo mass and yolk reserves compared to controls incubated at 37.5ºC. When the eggs were cooled to 20ºC regularly, the embryos had higher mass-specific metabolic rates and delayed development.

Peréz *et al.* (2008) experimentally heated the nests of the Tree Swallow (***Tachycineta bicolor***; Figure 20) during incubation. They found that incubating females maintained better body condition and fed nestlings at a greater rate. Their nestlings similarly had higher body mass and better body condition. In contrast, Ardia *et al.* (2008) examined the effects of cooling on the same species. They found that cooled eggs required longer incubation periods and the nestlings had a lower immunity to bacteria. Embryos that were exposed to experimental cooling resulted in nestlings that had lower residual and absolute body mass. The cooled females made fewer feeding trips, but this seemed to have no effect on nestling immunity to bacteria.

Figure 20. ***Tachycineta bicolor***, Tree Swallow, a species in which nest temperature affects health of the nestlings. Photo by John Benson, through Creative Commons.

One means by which birds can alter the temperature of a nest is by increasing its size or thickness. This mechanism is used by the Great Tit, ***Parus major*** (Figure 18-Figure 19) (Alabrudzińska *et al*. 2003). Clutch size (Figure 21) correlates negatively with total nest mass, but is positively correlated with the proportion of nest mass in the lining. Successful performances of eggs and nestlings are attributable to the quantity and proportion of moss in the nest structure as well as the nest size. Alabrudzińska and coworkers suggest that nest size and composition may affect moisture, temperature, protection, and/or sanitary conditions of the nest, thus supporting the hypothesis that mosses serve as more than structural materials.

Figure 21. ***Parus major***, Great Tit, nest with moss and eggs in nest box. Photo by Notts Ex Miner, through Creative Commons.

Deeming *et al*. (2012) extended this study to determine what triggers affect usage of more mosses in the nests of the Blue Tits (***Cyanistes caeruleus***; Figure 22) and Great Tits (***Parus major***; Figure 18-Figure 19, Figure 21). They found that nest mass is inversely related to temperatures experienced by the female during nest construction. Nest cup mass in particular is related to the temperatures experienced by the females during the seven days prior to the beginning of egg laying. This behavior is independent of latitude (Deeming *et al*. 2012), but nests are heavier at higher latitudes (Mainwaring *et al*. 2012).

Figure 22. ***Cyanistes caeruleus***, Blue Tit adult, feeding. Photo by Dave Howes, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36-Figure 37) can serve to illustrate the role nesting materials might play and give us some insight into the role mosses could play. The nest of the Sociable Weaver consists of multiple chambers, and in summer each chamber is occupied by 1-2 birds, whereas in winter there may be up to 5 birds in a chamber, with some chambers remaining empty (Bartholomew *et al.* 1976). Bartholomew and coworkers found that for the Sociable Weaver in the Kalahari Gemsbok National Park, South Africa, the nest temperatures varied only 7-8ºC when the outside temperatures ranged from 16-33.5ºC. This temperature is controlled largely by the number of birds in a chamber. Van Dijk *et al.* (2013) further found that nest volume had no effect on its thermoregulatory benefits. Nevertheless, the central part of the nest had the most stable conditions.

Blem and Blem (1994) suggested that the moist bryophytes could alter the nest temperature, presumably cooling it through evaporative cooling, and certainly maintaining a cool temperature longer against the hot (~43ºC) body temperature of the birds, much like a runner putting a wet band around his or her head. On the other hand, I suggest that the dark-colored mosses can also absorb sunshine like a dark body and warm the nest on cool days before leaves appear on the trees.

The nest of the **Prothonotary Warbler** (***Protonotaria citrea***; Figure 23), a cavity nester, consists of a cup made of grasses, leaves, and rootlets placed on a thick mat of moist, green bryophytes – both mosses and liverworts (Bent 1953; Petit 1989; Blem & Blem 1992). These bryophytes remain moist during the incubation and nestling stages (Blem & Blem 1994). It is likely that this nest composition affects the nest living conditions (Mertens 1977 a, b). The bryophyte composition of these nests ranges 74.7-80.2% of the dry mass of the nest. ***Anomodon attenuatus*** (Figure 24) is the most used of the five moss and two liverwort species. The other bryophytes found in nests were the mosses ***Haplocladium microphyllum*** (Figure 25), ***Amblystegium varium*** (Figure 26), ***Plagiomnium cuspidatum*** (Figure 27), and ***Thuidium delicatulum*** (Figure 28), and the liverworts ***Porella platyphylla*** (Figure 29) and ***Frullania eboracensis*** (Figure 30). The woven bryophyte nest is also able to expand as the baby birds grow, maintaining a tight fit to the tiny eggs, but expanding as the young birds grow.

Figure 23. ***Protonotaria citrea***, Prothonotary Warbler, a species that builds its nest on a mat of moist, green mosses. Photo by William H. Majoros, through Creative Commons.

Figure 24. ***Anomodon attenuatus***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 25. ***Haplocladium microphyllum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 26. ***Amblystegium varium***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 27. ***Plagiomnium cuspidatum***, a plagiotropic moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Michael Lüth, with permission.

Figure 28. ***Thuidium delicatulum***, a pleurocarpous moss used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Janice Glime.

Figure 29. ***Porella platyphylla***, a leafy liverwort that grows on rocks and trees and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Tim Waters through Creative Commons.

Figure 30. ***Frullania eboracensis***, a leafy liverwort that grows on bark and is used in nests of ***Protonotaria citrea***, the Prothonotary Warbler. Photo by Robert Klips, with permission.

Most of the evidence of the importance of bryophytes as insulators is inconclusive. Mainwaring *et al*. (2012) found that insulative properties of nest linings decreased as

the season progressed. The Blue Tit (***Cyanistes caeruleus***; Figure 22) exhibited seasonal changes in the nest composition, but the mass of mosses in the base of the nest showed no seasonal variation (Mainwaring *et al*. 2014). On the other hand, there was a seasonal decline in the mass of materials used to line the cup (Mainwaring & Hartley 2008).

Deeming and Mainwaring (2015) found that the Blue Tits (***Cyanistes caeruleus***; Figure 22), European Pied Flycatchers (***Ficedula hypoleuca***; Figure 31), and Common Redstart (***Phoenicurus phoenicurus***; Figure 32) used different nesting materials in the same types of nest boxes. Blue Tits used mostly mosses with hair, fur, and feathers (Figure 33); Flycatchers used leaves and grass (Figure 34); Redstarts used leaves, grass, moss, and lots of feathers. (Figure 35). Nevertheless, all three nest types have similar insulating properties.

Figure 31. ***Ficedula hypoleuca***, European Pied Flycatcher, a non-moss user. Photo by Ron Knight, through Creative Commons.

Figure 32. ***Phoenicurus phoenicurus***, Common Redstart, with earwig; this species uses mosses and other materials. Photo by Yerpo, through Creative Commons.

Figure 33. ***Cyanistes caeruleus***, Blue Tit, nest with mosses, feathers, and hair. Photo by Arnstein Ronning, through Creative Commons.

Figure 34. ***Ficedula hypoleuca***, European Pied Flycatcher, eggs with leaves and grass in the nest; mosses are not used. Photo by Arnstei Rønning, through Creative Commons.

Figure 35. ***Phoenicurus phoenicurus***, Common Redstart nest with moss, grasses, feathers, and eggs. Photo by Roberto Zanon, through Creative Common.

Humidity Control

Humidity control can be important for young birds, and nest materials can be used to buffer changes in humidity. We can use the Sociable Weaver (***Philetairus socius***; Figure 36) once more to illustrate this role, perhaps in the extreme.

Figure 36. ***Philetairus socius***, Sociable Weaver, a bird that builds a huge apartment nest that regulates humidity. Photo by Charles J. Sharp, through Creative Commons.

The Sociable Weaver (***Philetairus socius***; Figure 36) builds the largest bird nest (Figure 37) on the planet (van Dijk *et al*. 2013), housing at times over 100 pairs of birds (White *et al*. 1975). The nest is usually constructed in trees, using large twigs to construct the roof (Sociable Weaver 2017). Dry grasses separate the chambers and sharp spikes of straw deter predators from traversing the entrance tunnels. Inside, soft plant material, fur, cotton, and fluff line the nesting chambers. I can't help but wonder if bryophytes would be included if they were available in its habitat.

For the Sociable Weaver, the nest materials absorb the humidity, maintaining a lower humidity than that in the outside air (Bartholomew *et al.* 1976). The Sociable Weaver (***Philetairus socius***; Figure 36) does not use bryophytes, probably due to scarcity in its dry habitat, but where the bryophytes grow and are used by birds, I would expect them to have a significant role in absorbing and retaining humidity. I have taken bryophytes from a desiccator and watched their weight rise as I tried to weigh them. Bryophytes are able to take moisture out of the atmosphere, and thus they could also absorb moisture created by the birds' bodies. On the other hand, when the atmosphere is dry, the bryophytes could absorb moisture at night and help to keep baby birds, with scant covering of feathers, from drying out during the day.

Wimberger (1984) noted that the use of fresh bryophytes raised the humidity in nest cavities. This could prevent egg desiccation and increase hatching success (see also Clark & Mason 1985). On the other hand, the Fieldfare (***Turdus pilaris***; Figure 38-Figure 40) has an open nest, using grass and mud with very little moss or lichen. Compared to other species, the Fieldfare lost water rapidly. Within 10 minutes of removal of a water source, only 54% humidity remained in the nest, whereas the Redwing (***Turdus iliacus***; Figure 41) nest had 66%, the Eurasian Blackcap (***Sylvia atricapilla***; Figure 42-Figure 44) 71%, the Pied Flycatcher (***Ficedula hypoleuca***; Figure 31, Figure 34) 73%, the Chaffinch (***Fringilla coelebs***) 80%, and the Brambling (***Fringilla montifringilla***) 81%. Thrushes (**Turdidae**) made dense nests that still contained considerable water several days later. When the water content of the mosses and lichens was increased from 30% to 60%, the water content of the nest 24 hours later rose from 27% to 41%.

Figure 37. The very large nest of ***Philetairus socius***, Sociable Weaver. Photo by Harald Süpfle, through Creative Commons.

Figure 38. ***Turdus pilaris***, Fieldfare, with worm. This species uses little or no moss in its nest and the nest loses water rapidly. Photo by Grzegorz Golebiowski, through Creative Commons.

Figure 39. ***Turdus pilaris***, Fieldfare fledgling. Photo by Ernst Vikne, through Creative Commons.

Figure 40. ***Turdus pilaris***, Fieldfare, babies in nest – a species that uses few or no mosses in its nest. Photo by Arnstein Rønning, through Creative Commons.

Figure 41. ***Turdus iliacus***, Redwing, a bird that builds a nest that maintains moisture. Photo by Steve Garvie, through Creative Commons.

Figure 42. ***Sylvia atricapilla***, European Blackcap. Photo by S. Drozd Lund, through Creative Commons.

Figure 43. ***Sylvia atricapilla***, European Blackcap, a nest that is able to hold moisture. Photo by James K. Lindsey, with permission.

Figure 44. ***Sylvia atricapilla***, Eurasian Blackcap, nest with nestlings. Photo through Creative Commons.

Fontúrbel *et al*. (2020) noted that hummingbirds benefit from moisture retention by mosses, preventing eggs from drying out (see also Breil & Moyle 1976; Blem & Blem 1994).

In a study on passerine birds, Slagsvold (1989b) found that the width of the interior of the nest cup correlated negatively with the amount of mosses and lichens used in construction. It would seem, then, that using more mosses and narrowing the interior of the nest would provide a more insulated, more moist environment, and that bryophytes can be major contributors to those effects.

Elasticity

Elasticity can be important for both insulation and humidity. Slagsvold (1989a) noticed that the Chaffinch (***Fringilla coelebs***; Figure 45-Figure 46) and Brambling (***Fringilla montifringilla***; Figure 47) construct nest cups that expand in proportion to the number of young. This would also permit the nest to expand as the nestlings grow, continuing to maintain a warm blanket effect around them.

Slagsvold (1989a) considered selection for elastic nesting materials such as mosses and lichens as important criteria. But it appears that it is the ability to absorb rainwater rapidly, then to dry slowly, that is important.

Among the passerine birds, Slagsvold surmised that narrow nest cups were especially common with small-sized birds that nest above ground. These nests are typically open and include large quantities of mosses and lichens.

Figure 45. ***Fringilla coelebs***, Chaffinch, a bird that selects nesting materials, such as bryophytes, that expand as nestlings grow. Photo by Andreas Trepte, through Creative Commons.

Figure 46. ***Fringilla coelebs***, Chaffinch, expandable nest with mosses. Photo by Trachemys, through Creative Commons.

Figure 47. ***Fringilla montifringilla***, Brambling male, a species for which mosses keep the nest moist. Photo by M. M. Lolek, through Creative Commons.

Antibacterial, Antiparasitic?

There are lots of hungry predators, albeit tiny, that enjoy living on birds. These can take a toll on survival. Adults and juveniles of the Cliff Swallow (***Petrochelidon pyrrhonota***; Figure 48) occupying parasite-free (fumigated) colonies had an average of 4.4% (adults) and 62.2% (juveniles) greater daily survival than their counterparts in naturally infested colonies (Brown & Brown 2004). Several researchers (Wimberger 1984; Clark & Mason 1985) suggest that the bryophytes may serve as insecticidal and anti-pathogenic agents in the nest. Clark and Mason examined the European Starling (***Sturnus vulgaris***; Figure 49) as a likely recipient of such help because it uses the same nest for multiple years, thus increasing the chances for parasite and pathogen encounter. This species chooses fresh green material in its nest, restricting its selection to a small number of species and choosing plants with volatile compounds that are likely to inhibit arthropod hatching or bacterial growth. These plants typically possess greater concentrations of mono- and sesquiterpenes than the local flora in general.

Figure 48. ***Petrochelidon pyrrhonota***, Cliff Swallow, a bird that has lots of parasites. Photo by Ingrid Taylar, through Creative Commons.

Figure 49. ***Sturnus vulgaris***, European Starling, a species that re-uses its nest and incorporates plants that contain greater concentrations of mono- and sesquiterpenes than the local flora in general. Photo by Luzmaria, through Creative Commons.

Igic *et al*. (2009) found that the Song Thrush (***Turdus philomelos***; Figure 50) used cigarette butts in its nest (Figure 51). This raised the question of anti-predatory nesting materials, as shown by Strecker (1926) and Schuetz (2005) for shed snake skins and carnivore scat. But mosses and odiferous leaves may serve this function as well, protecting birds against ectoparasites (Clark & Mason 1988; Banbura *et al*. 1995; Lambrechts & Santos 2000).

Figure 50. ***Turdus philomelos***, Song Thrush, a bird that may use anti-predatory nesting material. Photo by Yvan, through Creative Commons.

Figure 51. ***Turdus philomelos***, Song Thrush, feeding babies in New Zealand nest. Photo from ZipCodeZoo, through Creative Commons.

Blue Tits (***Cyanistes caeruleus***; Figure 22) use odor cues to determine when to replace green plant materials (Mennerat 2008). The female Blue Tits bring fresh plants to their nests (Banbura *et al*. 1995), so there is reason to believe that these plants may be chemically endowed in a way that helps to protect the nest. Both parents hesitated longer before entering the nest box when the experimenter added green tracheophyte material compared to addition of mosses. Banbura concluded that we cannot rule out antiparasite functions of green plant material in the Blue Tit nests, but neither can we say conclusively that they serve this purpose.

On Corsica, Mennerat *et al*. (2009a, b) found that despite adding aromatic plants to their nests, the Blue Tit (***Cyanistes caeruleus***; Figure 22) experiences just as many parasites as without them. However, their growth is improved. The researchers found that the bacterial community in the nest was significantly affected by these plants, being reduced on nestlings. This offered the further advantage that the bacteria reduced most on the chicks with the worst infestations of the blood-sucking blowfly larvae (*Protocalliphora*). On the other hand, birds in nests where aromatic plants were replaced by mosses did not experience the benefits experienced in accompaniment of the aromatic plants: chick mass gain, higher haematocrit levels, faster feather development (Mennerat *et al.* 2009b).

Shutler and Campbell (2007) added greenery to nests of the non-greenery-using Tree Swallows (***Tachycineta bicolor***; Figure 20). They found no evidence that feathers had reduced parasites, but the added green plant material did result in lower numbers of ectoparasites in the nests. Nevertheless, there was no increase in breeding success.

Dawson *et al*. (2011) investigated the use of feathers to line nests in the Tree Swallow (***Tachycineta bicolor***; Figure 20). They found that adding feathers to nests actually increased the abundance of ectoparasites in those nests, a conclusion previously noted by Lombardo *et al.* (1995). Dawson and coworkers interpreted this to mean that the feathers separated the nestlings from the parasites. This conclusion supported that of Winkler (1993) in a study that showed that removal of feathers from Tree Swallow nests caused higher mite and lice infestation on nestlings, coinciding with lower growth rates of the nestlings, compared to controls. But there is also a cost to males that spend more time to gather more feathers – they are more likely to lose their mate to another male!

Wimberger (1984) further showed that birds in **Falconiformes** that used their nests in successive years were more likely to include green foliage, including bryophytes, than those species that did not reuse their nests. This suggests that the bryophytes may have some sort of protective function.

If birds choose nesting materials based on their antibiotic properties, it would seem that they would need to detect the odors caused by the compounds that facilitate this antibiotic use. But the **Passeriformes** (the birds that more often use bryophytes in their nests) are known to have a very small relative **olfactory** (odor-sensing) bulb size (Mennerat *et al*. 2005). Thus we have assumed that these birds have poor olfactory senses.

It appears that this wisdom is misleading, at least for some passerine birds (Mennerat *et al*. 2005; Strandh *et al.* 2012). The Blue Tit (***Cyanistes caeruleus***; Figure 22) uses mosses in her nest and this species is one of the birds that is sensitive to the odor of lavender (Mennerat *et al*. 2005). If birds choose vegetation based on the odor of volatile compounds, then I am surprised that the aromatic thallose liverworts do not seem to be used in nests.

Brian Dykstra (pers. comm. 10 December 2011) asked an interesting question. Liverworts such as species of ***Frullania*** (Figure 30) often house rotifers in their lobules (Figure 52). Could it be that these bacteria consumers actually help the birds by reducing the abundance of pathogens?

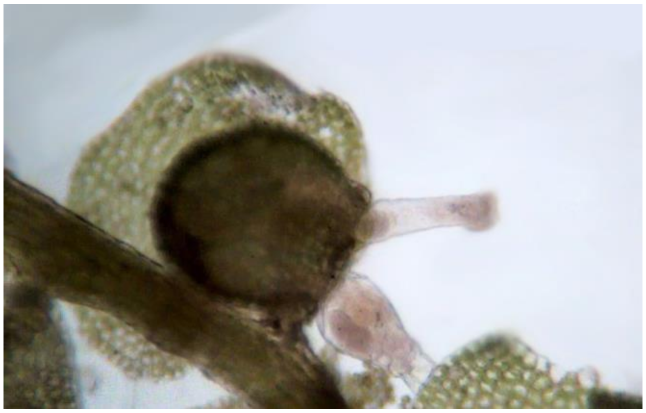

Figure 52. ***Frullania eboracensis*** lobule with rotifer. Photo courtesy of Lisa Pokorski.

We know that bryophytes themselves often have antibacterial properties (*e.g.* Basile *et al.* 1999; Alabrundzinska *et al.* 2003; Ariyo *et al*. 2011; Bukvicki *et al*. 2012; Asakawa *et al*. 2013; Yu *et al.* 2014), but until now, no study has demonstrated conclusively that they serve this purpose in the nests of birds.

At last, Fontúrbel *et al*. (2020) have shown that "Mamma knows best." They found that the hummingbird Picaflor Rubi (***Sephanoides sephaniodes***; Figure 53-Figure 54) selects the mosses ***Ancistrodes genuflexa*** (in 100% of the nests; Figure 55), ***Weymouthia mollis*** (27%; Figure 56), and ***Weymouthia cochlearifolia*** (17%; Figure 57) based on samples in austral South America, but ***A. genuflexa*** is particularly scarce in the forest while comprising up to 97% of the moss nesting material. They identified five compounds with antibacterial properties (Figure 58) in ***A. genuflexa***.

Figure 53. ***Sephanoides sephaniodes***, a hummingbird that uses ***Ancistrodes genuflexa*** selectively in its nests, giving the nests antibiotic properties. Photo by Felipe Bernala, through Creative Commons.

Figure 54. ***Sephanoides sephaniodes*** nest made with mosses. Photo by Diucón, through Creative Commons.

Figure 55. ***Ancistrodes genuflexa***, the most common moss in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Felipe Osorio Zúñiga, with permission.

Figure 56. ***Weymouthia mollis***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission

Figure 57. ***Weymouthia cochlearifolia***, a moss used in nests of Picaflor Rubi (***Sephanoides sephaniodes***). Photo by Juan Larrain, with permission.

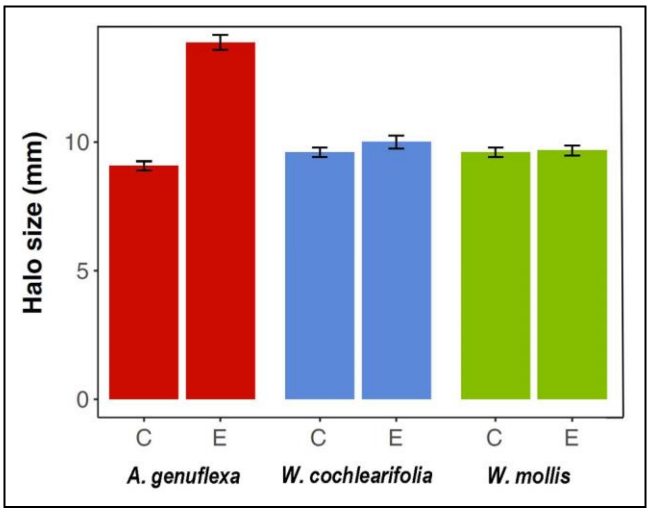

Figure 58. Antimicrobial activity of control (**C**) and moss extracts (**E**) from ***Ancistrodes genuflexa***, ***Weymouthia mollis***, and ***Weymouthia cochlearifolia***) against five common bacteria strands. Error bars represent standard error. Modified from Fontúrbel *et al*. 2020.

We know from other studies that birds may prefer materials that have antibiotic properties. Doctoral student Sarah Knutie became curious when one of Darwin's finches (Figure 59) pulled at cotton threads on the clothes line rope to use as nesting material (Pety 2020). She followed up with an experiment using cotton balls. Half of them had antibiotic solution (1% permethrin) and half had just water. These were available in wire-mesh dispensers. Of the 26 active nests examined, 85% contained cotton. Of these, 13 nests had permethrin-treated cotton and 9 had untreated cotton. Only 4 had no cotton. Of the 8 nests with at least 1 g of treated cotton, 7 had no parasites and the eighth had only 4. Hence, it appears that the birds may select materials with antibiotic properties. That could explain at least some of the selection of bryophytes for nesting material.

Figure 59. Darwin's finch with bryophytes in its beak, a bird that sometimes collects cotton balls with antibiotics for nesting. Photo by Rudy R., through Creative Commons.

There is a wide array of research projects needed to understand the role of bryophytes in nests. What is their elasticity compared to other nesting materials? Do they provide antibiotic properties that reduce parasites, fungi, or bacteria? Do they serve as better insulators than other materials? Do they keep the nest at a more constant humidity than other materials? Are they easier to work with or to carry than other materials?

Cavity Nest Elevation

Bryophytes have an additional function for cavity-nesting birds. They are often used to raise the nest cup so that the baby birds can be reached easily by the parents when feeding the birds and the birds can get in and out easily (Hamao *et al*. 2016). The bryophytes can also serve to separate the nest cups from cavity walls that may remain too moist, at the same time absorbing the excess moisture (Hamao *et al*. 2016).

Selection of Nest Materials

Just how choosy are the birds about the mosses they use? Breil and Moyle (1976) found that 11 birds had used 60 different species of mosses, including aquatic species, in their nests, suggesting that preference may simply depend on availability. Pant (1989) investigated the nests of five bird species in the Kumaon Himalaya and found that the primary mosses used were pleurocarpous. He supposed that these were preferred because they were easier to shape to suit the shape of the nest. This might also account for the use of larger leafy liverworts, in addition to pleurocarpous mosses, in the nest of the Streaked Laughing Thrush (***Trochalopteron lineatum***; Figure 60) (Pant & Tewari 1984). Furthermore, Abolina (1991) found that the large leafy liverworts ***Radula complanata*** (Figure 61) and ***Lophocolea heterophylla*** (Figure 62) were used for nesting material in Lithuania.

In their study of nests of twelve bird species, Breil and Moyle (1976) found that most birds chose the bryophytes that were most abundant locally. These included the aquatic mosses ***Fontinalis*** (Figure 63) and ***Hygrohypnum*** (Figure 64), and ***Sphagnum*** (Figure 16). Terrestrial mosses were mostly the pleurocarpous ***Brachythecium***

(Figure 65), ***Hedwigia*** (Figure 66), and ***Thuidium*** (Figure 67), plus the epiphytic bryophytes ***Frullania*** (Figure 30) and ***Platygyrium repens*** (Figure 68).

Figure 60. ***Trochalopteron lineatum***, Streaked Laughing Thrush, one of the few birds known to use leafy liverworts in its nest. Photo by P. Jeganathan, through Creative Common.

Figure 61. ***Radula complanata***, a nesting material for birds in Lithuania. Photo by Hermann Schachner, through Creative Commons.

Figure 62. ***Lophocolea heterophylla***, a nesting material for birds in Lithuania. Photo by Bob Klips, with permission.

Figure 63. ***Fontinalis antipyretica***; some members of this genus are used in bird nests. Photo by Andrew Spink, with permission.

Figure 64. ***Hygrohypnum ochraceum***, ; some members of this genus are used in bird nests. Photo by Michael Lüth, with permission.

Figure 65. ***Brachythecium rutabulum***, representing a genus commonly used in bird nests. Photo by Kristian Peters, through Creative Commons.

Figure 66. Dry ***Hedwigia ciliata*** with capsules, a pleurocarpous species commonly used in bird nests. Photo by Hugues Tinguy, through Creative Commons.

Figure 67. ***Thuidium delicatulum***, representing a genus commonly used in bird nests. Photo by Janice Glime.

Figure 68. ***Platygyrium repens***, an epiphytic moss commonly used in bird nests in the Appalachians, USA. Photo by Hermann Schachner, through Creative Commons.

Other birds appear to be especially choosy. In Hawaii, one bird nest (most likely of a non-native species) made its nest almost entirely from the setae and capsules of ***Pyrrhobryum*** (***Rhizogonium***) ***spiniforme*** (Figure 69-Figure 70) (Brandon Stone, Bryonet 9 April 2003).

Figure 69. ***Pyrrhobryum spiniforme***, a moss used exclusively in some bird nests in Hawaii. Photo by Alan Cressler, with permission.

Figure 70. ***Pyrrhobryum spiniforme*** with capsule and seta that are used for nests by some birds in Hawaii. Photo by Janice Glime.

In the Uluguru Mountains of Tanzania, Tamás Pócs (Bryonet 2 June 2010) observed a nest of a small bird made purely of ***Orthostichella rigida*** (Figure 71), a common hanging epiphyte.

Figure 71. ***Orthostichella rigida*** from Tasmania, a pendent moss used in bird nests there. Photo courtesy of Tamás Pócs.

In Kenya, Min Chuah Petiot (Bryonet 2 June 2010) has collected an abandoned and fallen nest made with the hanging moss ***Papillaria africana*** (Figure 72). This moss was still green and alive.

Figure 72. ***Papillaria africana***, nesting material in Kenya. Photo by Bruno Senterre, with permission.

Gustavo Tomás and Andrew Spink (Andrew Spink, Bryonet 2 June 2010) collected moss samples from a large number of Blue Tit (***Cyanistes caeruleus***; Figure 22) and Coal Tit (***Periparus ater***; Figure 73) nests from a woodland in the eastern Netherlands. The most common species in nests was ***Hypnum cupressiforme*** (Figure 74-Figure 75), which is common in the area. However, other locally common mosses were less common in the nests, indicating that the birds clearly selected certain species. It is interesting that different species were used in different parts (top/bottom) of the nest.

Figure 73. ***Periparus ater***, Coal Tit, a species that commonly uses ***Hypnum cupressiforme*** (Figure 74) in its nests in The Netherlands. Photo from Biopix, through Creative Commons.

Figure 74. ***Hypnum cupressiforme***, a moss commonly used in nests of Blue Tits and Coal Tits, covering the log. Photo by Michael Lüth, with permission.

Figure 75. ***Hypnum cupressiforme*** var ***cupressiforme***, a preferred moss in nests of Blue Tits and Coal Tits. Photo by David Holyoak, with permission.

In the Pacific Northwest of Oregon and Washington, all seven thrush species (**Turdidae**) and six hummingbird species (**Trocholidae**) use either bryophytes or lichens in their nests (Wolf 2009). All nine crows and jays (**Corvidae**) except the Black-billed Magpie (***Pica hudsonia***; Figure 76-Figure 77) use bryophytes for nesting material. These Pacific Northwest bryophytes include ***Alsia*** (Figure 78), ***Brachythecium*** (Figure 65), ***Calliergon*** (Figure 79), ***Dendroalsia*** (Figure 80), ***Dicranum*** (Figure 81), ***Eurhynchium*** (Figure 82), ***Homalothecium*** (Figure 83), ***Hypnum*** (Figure 74), ***Isothecium*** (Figure 84), ***Pogonatum*** (Figure 85), ***Pohlia*** (Figure 91), ***Polytrichum*** (Figure 86), ***Porella*** (Figure 88), and ***Sphagnum*** (Figure 87).

Figure 76. ***Pica hudsonia***, Black-billed Magpie, a bird that does not use bryophytes in its nest. Photo by Carplips, through Creative Commons.

Figure 77. ***Pica hudsonia***, Black-billed Magpie, nest showing mud and vegetable matter, but no bryophytes. Photo by Rich Mooney, through Creative Commons.

Figure 78. ***Alsia californica*** with capsules, a moss used in nests in the Pacific Northwest, USA. Photo by Paul Wilson, with permission.

Figure 79. ***Calliergon giganteum*** with ice, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Kristian Peters, through Creative Commons.

Figure 80. ***Dendroalsia abietina***, a species used commonly in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 81. ***Dicranum scoparium***, one of the mosses available for use in bird nests in the Pacific Northwest, USA. Photo by J. C. Schou, through Creative Commons.

Figure 82. ***Eurhynchium praelongum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

Figure 83. ***Homalothecium sericeum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Michael Lüth, with permission.

Figure 84. ***Isothecium myosuroides***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Dale Vitt, with permission.

Figure 85. ***Pogonatum urnigerum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Janice Glime.

One commonality to surmise from these studies is that short, acrocarpous mosses are rarely used. In the first report of bryophytes in bird nests in Chin, Cao and Gao (1991) found only pleurocarps among the 18 species used. These were mostly hanging mosses in **Meteoriaceae** (Figure 71), **Pterobryaceae** (Figure 89), and **Trachypodaceae** (Figure 90). Mosses that are long, mostly pleurocarpous species or those with a **plagiotropic** (growing inclined or nearly horizontally) habit, and larger

leafy liverworts comprise almost all of the bryophytes in bird nests. (Most leafy liverworts grow horizontally.)

Figure 86. ***Polytrichum juniperinum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Vincent de Boer, through Creative Commons.

Figure 87. ***Sphagnum fimbriatum***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by David T. Holyoak, with permission.

Figure 88. ***Porella navicularis***, in a genus used in bird nests in the Pacific Northwest, USA. Photo by Rosemary Taylor, with permission.

Figure 89. ***Pterobryon densum*** (**Pterobryaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Michael Lüth, with permission.

Figure 90. ***Bryowijkia ambigua*** (**Trachypodaceae**), in one of the three most common bryophyte families in Chinese bird nests. Photo by Li Zhang, with permission.

Even in the case of the acrocarpous moss ***Pohlia nutans*** (Figure 91) in a nest, it was only the sporophytes that were used (Crum 1973). Mrs. Cuthbert, of Mount Pleasant, Michigan, USA, reported that she found a bird nest lined with moss sporophytes (a hundred or so, as in Figure 92), giving a gold-colored look to the interior on a wet day (Crum 1973). Crum identified the moss as ***Pohlia nutans*** (Figure 91).

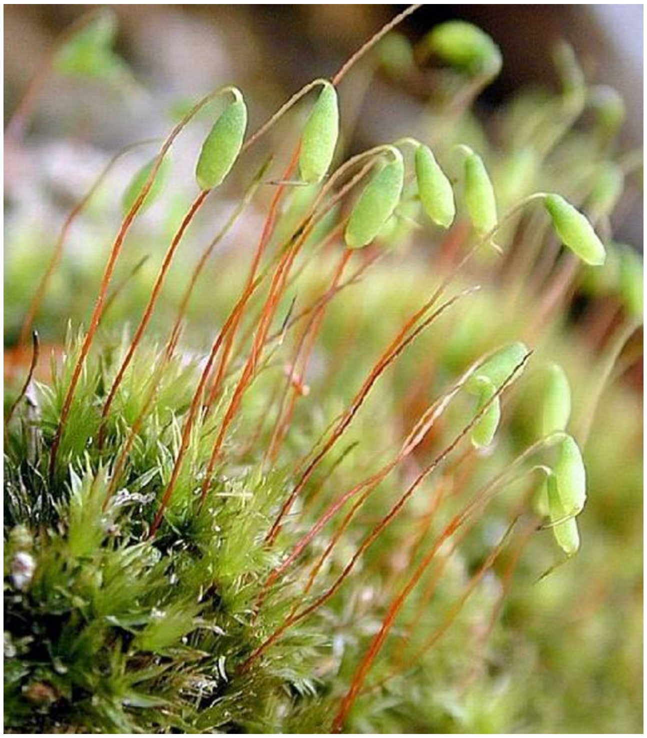

Figure 91. ***Pohlia nutans*** with capsules; setae of this moss are used in some bird nests. Photo by Michael Lüth, with permission.

Figure 92. Nest with sporophyte setae and capsules, possibly from ***Pohlia nutans*** (Figure 91). Photo courtesy of Lovatt.

Who Uses Mosses in Nests?

Breil and Moyle (1976) examined a number of nests of 12 eastern USA birds, identifying 65 species of mosses used in construction. They reported that all North American passerine birds use bryophytes in their nests, emphasizing the importance of bryophytes as an ecosystem component. These 65 species of bryophytes included 5 species of leafy liverworts. Of the nests examined, only the Indigo Bunting (***Passerina cyanea***; Figure 93) nest (Figure 94) lacked bryophytes.

Wolf (2009) conducted an extensive survey of bryophyte usage by birds in the Pacific Northwest (Oregon and Washington), USA. These are listed by orders, along with other records, in the following nest subchapters.

Figure 93. ***Passerina cyanea***, Indigo Bunting, on moss, although it did not include these in its nest in the eastern USA study. Photo by Steve Trynoski, with permission.

Figure 94. ***Passerina cyanea***, Indigo Bunting, nest with eggs, showing total lack of bryophytes. Photo by Richard Bonnett, through Creative Commons.

Summary

Birds often use bryophytes in their nests. This inclusion may help to maintain a safe temperature, to maintain suitable moisture, to prevent disease and parasitism, to provide a soft lining, to camouflage the nest, to permit the nest to expand as nestlings grow, and to help hold the nest together.

The use of bryophytes in nests is much more common among the **Passeriformes** (perching birds) than among the other orders of birds. Some birds are very specific in their choices, using only one or a few species when many are in the area. Most birds choose bryophytes with a plagiotropic growth habit and avoid acrocarpous mosses. Some select sporophytes, especially setae, to serve as nest linings.

What is clear is that we know little about the advantages that bryophytes may give birds when the bryophytes are included in the nests.

Acknowledgments

Thank you to Brian Dykstra for sending me the wonderful thesis on birds and epiphytes by Adrian Wolf, as well as other references and personal observations. David Dumond shared the references he got from Bryonetters. Tamás Pócs took a number of pictures of ***Orthostichella rigida*** just for this project. Thank you to Janet Marr for a critical reading of the manuscript.

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CHAPTER 16-4
BIRD NESTS – NON-PASSERIFORMES, PART 1

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CHAPTER 16-4 BIRD NESTS – NON-PASSERIFORMES, PART 1

Figure 1. Bird nest among ferns, with mosses surrounding nest cup. Photo courtesy of JeriLynn Peck.

Anseriformes Screamers, Ducks, *etc*

Anatidae – Swans, Geese, & Ducks

Wolf (2009) found eleven species of **Anatidae** that use bryophytes in their nests in North America:

Anser brachyrhynchus (Pink-footed Goose; Figure 2-Figure 3)
Anser albifrons (Greater White-fronted Goose; Figure 4-Figure 5)
Branta bernicla (Brant; Figure 6-Figure 7)
Branta canadensis (Canada Goose; Figure 8-Figure 10)
Cygnus columbianus (Tundra Swan; Figure 11-Figure 12)
Cygnus cygnus (Whooper Swan; Figure 13)
Aythya collaris (Ring-necked Duck; Figure 14)
Clangula hyemalis (Long-tailed Duck; Figure 15-Figure 20)
Mergus merganser (Common Merganser; Figure 23)
Somateria fischeri (Spectacled Eider; Figure 24-Figure 26)
Somateria mollissima (Common Eider; Figure 27)

Pink-footed Goose (*Anser brachyrhynchus*)

The Pink-footed Goose (***Anser brachyrhynchus***) may use bryophytes in the nest in parts of North America. But in the Arctic they choose dry vegetation patches for their nests. Having moist bryophytes nearby is important in nest selection sites, however. These bryophyte areas are used for foraging (Jensen *et al*. 2008; Wisz *et al*. 2008).

Figure 2. ***Anser brachyrhynchus***, Pink-footed Goose, a bird that uses bryophytes in its nests in North America. Photo by Hilary Chambers, through Creative Commons.

Figure 3. ***Anser brachyrhynchus***, Pink-footed Goose, on mossy nest. Photo by Otto Plantema, with permission.

Figure 4. ***Anser albifrons***, Greater White-fronted Goose, a species that uses mosses in their nests in North America. Photo by John B., through Creative Commons.

Figure 5. ***Anser albifrons albifrons***, White-fronted Goose, on nest. Photo by Tim Bowman, USFWS, through public domain.

Figure 6. ***Branta bernicla***, Brant, a species that uses mosses in their nests in parts of North America Photo by Jeroen Reneerkens, through Creative Commons.

Figure 7. ***Branta bernicla***, Brant, nest with eggs. Photo by Bob Gill, USFWS, through public domain.

Figure 8. ***Branta canadensis***, Canada Goose, a species that uses mosses in their nests in North America. Photo courtesy of Eileen Dumire.

Figure 9. ***Branta canadensis***, Canada Goose, nest with eggs and down lining. Photo by James K. Lindsey, with permission.

Figure 10. ***Branta canadensis***, Canada Goose, nest with no special lining, demonstrating differences one can find among nests (compare to Figure 9). Photo by Notts Ex Miner, through Creative Commons.

Figure 11. ***Cygnus columbianus***, Tundra Swan, a species that uses bryophytes in their nests in North America and elsewhere. Photo by Tim Bowman, through public domain.

Figure 12. ***Cygnus columbianus***, Tundra Swan, on nest. Photo from USFWS, through public domain.

Figure 13. ***Cygnus cygnus***, Whooper Swans, a species that uses bryophytes in their nests in North America. Photo by Sciadopitys, through Creative Commons.

Figure 14. ***Aythya collaris***, Ring-necked Duck, on water, a species that uses bryophytes in their nests in North America. Photo by MDF, through Creative Commons.

Long-tailed Duck (*Clangula hyemalis*)

I suspect that bryophytes are not the normal nesting material for the Long-tailed Duck (***Clangula hyemalis***; Figure 15-Figure 16). Its nest is typically built on the ground near water, using vegetation and lined with down (Wikipedia 2016). But Susan Studlar (pers. comm. 12 July 2017) reported to me that they built large nests (Figure 17-Figure 20) of ***Rhytidiadelphus*** cf. ***loreus*** (Figure 21) when that was the only material provided to them at the Sealife Center in Seward, Alaska. I suspect most birds are adaptable, using the materials that are most available to them at the time of nest building. The Horned Puffin (***Fratercula corniculata***; Figure 22), on the other hand, ignores all those mosses in the landscape and lays its eggs in a crevice among the rocks (Wikipedia 2017).

Figure 15. ***Clangula hyemalis***, Long-tailed Duck, a species that uses bryophytes in their nests in North America. Photo by Wolfgang Wander, through Creative Commons.

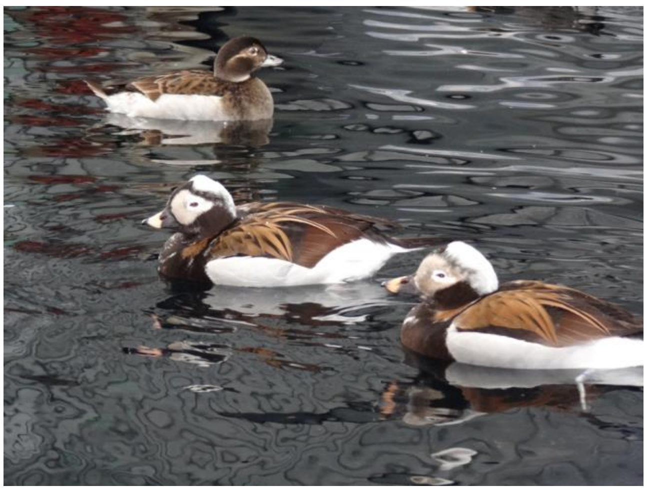

Figure 16. ***Clangula hyemalis***, Long-tailed Duck, a species that will use mosses to build a nest when other materials are not available. Photo courtesy of Sue Studlar.

Figure 17. ***Clangula hyemalis***, Long-tailed Duck, female on nest. Photo by Tim Bowman, USFWS, through public domain.

Figure 18. ***Clangula hyemalis***, Long-tailed Duck, on nest on a bed of mosses. Photo through public domain.

Figure 19. ***Clangula hyemalis***, Long-tailed Duck, nest made of ***Rhytidiadelphus*** cf. ***loreus*** – the only material available to it. Photo courtesy of Sue Studlar.

Figure 20. ***Clangula hyemalis***, Long-tailed Duck, ***Rhytidiadelphus*** cf. ***loreus*** nest lined with down. The moss was the only material provided to it. Photo courtesy of Sue Studlar.

Figure 21. ***Rhytidiadelphus*** cf. ***loreus*** in nest of ***Clangula hyemalis*** (Long-tailed Duck). Photo courtesy of Sue Studlar.

Figure 22. ***Rhytidiadelphus*** cf. ***loreus*** and Horned Puffin (***Fratercula corniculata***) in Seward, Alaska. The moss looks inviting, but the Puffin usually lays its one egg in a crevice or cavity among the rocks without a nest. Photo courtesy of Sue Studlar.

Figure 23. ***Mergus merganser***, Common Merganser, a species that uses bryophytes in their nests in North America. Photo by John Bennett, through Creative Commons.

Figure 24. ***Somateria fischeri***, Spectacled Eider female, a species that uses bryophytes in their nests in North America. Photo by Dick Daniels, through Creative Commons.

Figure 25. ***Somateria fischeri***, Spectacled Eider pair, a species that uses bryophytes in their nests in North America. Photo by Laura Whitehouse, USFWS, through public domain.

Figure 26. ***Somateria fischeri***, Spectacled Eider, nest. Photo by USFWS, through public domain.

Figure 27. ***Somateria mollissima***, Common Eider, colonial nesting with Canada geese. Photo by Caroline Bond, USGS, through public domain.

Snow Goose (*Chen caerulescens*)

It is not surprising to find that in the far north, where mosses are a prominent feature of the landscape, birds like the Snow Goose (***Chen caerulescens***; Figure 28) use mosses as a major component of their nests (Figure 29) (Gianetta 2000). The Greater Snow Goose (***Chen caerulescens atlanticus***; Figure 30) in Jungersen Bay, northern Baffin Island, uses three habitat types for nesting (Giroux *et al*. 1984). One of these is wet moss-covered meadows with up to 5 cm of standing water, dominated by *Carex aquatilis* var. *minor* (Figure 31), *Dupontia fisheri* (Figure 32), *Calamagrostis stricta* (Figure 33), and *Arctagrostis latifolia* (Figure 34).

Figure 29. ***Chen caerulescens***, Snow Goose, nest with nestlings and often containing bryophytes. Photo by James K. Lindsey, with permission.

Figure 30. ***Chen caerulescens atlanticus***, Greater Snow Geese foraging. Photo by D. Gordon and E. Robertson, through Creative Commons.

Figure 28. ***Chen caerulescens*** (Snow Goose) grazing; this species uses mosses as a major component of their nests. Photo by Walter Siegmund, through Creative Commons.

Figure 31. ***Carex aquatilis*** var ***minor*** in the Northwest Territories, common in the home of the Greater Snow Goose. Photo by Jeffery M. Saarela, through Creative Commons.

Figure 32. ***Dupontia fisheri***, common in the habitat of the Greater Snow Goose. Photo from Smithsonian Institution, National Museum of Natural History, through Creative Commons.

Figure 33. ***Calamagrostis stricta*** in the Northwest Territories, common in the habitat of the Greater Snow Goose. Photo by Matt Lavin, through Creative Commons.

Figure 34. ***Arctagrostis latifolia*** subsp. ***latifolia*** in the Northwest Territories, common in the habitat of the Greater Snow Goose. Photo by Jeffery M. Saarela, through Creative Commons.

McCracken *et al.* (1997) found that among the Ross' Geese (***Chen rossii***; Figure 35) and Lesser Snow Geese (***Chen caerulescens caerulescens***; Figure 37), the nest size (Figure 36) differed with habitat. The smallest were among heath, then rock, then mixed, with the largest nests among mosses. Temperature was an important factor for these Arctic breeders. Could it be that mosses tended to insulate the eggs, but at the same time prevented the warmer temperatures that could speed up development? Were the mosses too compact and tight to be good insulators? Or did the mosses indicate a cooler ground temperature?

Figure 35. ***Chen rossii***, Ross's Snow Goose, a species whose nest size is largest when among mosses. Photo by Dominic Sherony, through Creative Commons.

Figure 36. ***Chen rossii***, Ross' Goose, nest with mosses and eggs. Photo by James K. Lindsey, with permission.

Figure 37. ***Chen caerulescens caerulescens***, Lesser Snow Goose, a species that makes larger nests among mosses than among heath vegetation. Photo by Walter Siegmund, through Creative Commons.

Phasianidae – Quail, Pheasants, *etc*

Wolf (2009) found five species of **Phasianidae** that use bryophytes in their nests in parts of North America:

Falcipennis canadensis (Spruce Grouse; Figure 38-Figure 39)
Lagopus lagopus (Willow Ptarmigan; Figure 40-Figure 42)
Lagopus muta (Rock Ptarmigan; Figure 43-Figure 44)
Dendragapus obscurus (Blue Grouse; Figure 45-Figure 46)
Tympanuchus phasianellus (Sharp-tailed Grouse; Figure 47-Figure 48)

Figure 38. ***Falcipennis canadensis***, Spruce Grouse, on mossy log. Photo by MDF, through GNU Free Documentation.

Figure 39. ***Falcipennis canadensis***, Spruce Grouse, nest with eggs. Photo by Mark Yezbick and Willi Shrinx, through Creative Commons.

Figure 40. ***Lagopus lagopus***, Willow Ptarmigan female, among mosses in Alaska, a species that uses bryophytes for nesting. Photo by David Menke, USFWS, through Creative Commons.

Figure 41. ***Lagopus lagopus***, Willow Ptarmigan nest with eggs. Photo by James K. Lindsey, with permission.

Figure 42. ***Lagopus lagopus***, Willow Ptarmigan, nest among mosses. Photo by Mlkniemi, through Creative Commons.

Figure 43. ***Lagopus muta***, Rock Ptarmigan, a species that uses bryophytes for nesting. Photo by Friedrich Böhringer, through Creative Commons.

Figure 44. ***Lagopus muta***, Rock Ptarmigan, nest. Photo by Valugi, through Creative Commons.

Figure 45. ***Dendragapus obscurus***, Blue Grouse, a species that uses bryophytes in their nests in North America. Photo by S. King, NPS, through public domain.

Figure 46. ***Dendragapus obscurus***, Blue Grouse, male. Photo from USNPS, through public domain.

Figure 47. ***Tympanuchus phasianellus***, Sharp-tailed Grouse, a species that uses bryophytes in their nests in parts of North America. Photo by Barbara Muenchau, through Creative Commons.

Figure 48. ***Tympanuchus phasianellus***, Sharp-tailed Grouse, nest with eggs. Photo from USFWS, through public domain.

Gaviiformes: Loons

Gaviidae – Loons

Wolf (2009) found three species of **Gaviidae** that use bryophytes in their nests in parts of North America:

Gavia stellata (Red-throated Loon; Figure 49)
Gavia pacifica (Pacific Loon; Figure 50)
Gavia immer (Common Loon; Figure 51-Figure 52)

Figure 49. ***Gavia stellata***, Red-throated Loon on nest. Photo by Dave Menke, through public domain.

Figure 50. ***Gavia pacifica***, Pacific Loon, on nest. Mosses may be included in these nests. Photo from USFWS, through public domain.

Figure 51. ***Gavia immer***, Common Loon, with chick. Photo from NPS, through public domain.

Figure 52. ***Gavia immer***, Common Loon, on nest. Photo by Dana Moos, through Creative Commons.

Podicepidiformes: Grebes

Podicepididae – Grebes

Red-Necked Grebe (*Podiceps grisegena*)

Breeding populations of the **Red-necked Grebe**, ***Podiceps grisegena*** (Figure 53), in the Northwest Territories use ***Sphagnum*** (Figure 107) in addition to cattails and other emergent vegetation in nest construction (Figure 54) (Fournier & Hines 1998).

Figure 53. ***Podiceps grisegena***, Red-necked Grebe, with ducklings. Photo by Donna Dewhurst, through public domain.

Figure 54. ***Podiceps grisegena***, Red-necked Grebe, a species that includes ***Sphagnum*** in their nests. Photo by Lukasz Lukasik, through Creative Commons.

Pelecaniformes: Tropicbirds, Pelicans, *etc*

Phalacrocoracidae – cormorants

Wolf (2009) found two species of **Phalacrocoracidae** that use bryophytes in their nests in North America:

Phalacrocorax penicillatus (Brandt's Cormorant; Figure 55)
Phalacrocorax pelagicus (Pelagic Cormorant; Figure 56-Figure 57)

Figure 55. ***Phalacrocorax penicillatus***, Brandt's Cormorants, on nests. Photo by Franco Folini, through Creative Commons.

Figure 56. ***Phalacrocorax pelagicus***, Pelagic Cormorant, female and chicks on nest. This species uses bryophytes in their nests in parts of North America. Photo by Alan Vernon, through Creative Commons.

Figure 57. ***Phalacrocorax pelagicus***, Pelagic Cormorant, on nest. Photo by Alan Vernon, through Creative Commons.

Falconiformes: Vultures, Hawks, & Falcons

Accipitridae – Hawks, Old World Vultures & Harriers

Despite their large size and predatory habits, Wolf (2009) found seven species of **Accipitridae** that use bryophytes in their nests in the Pacific Northwest of the USA.:

Aquila chrysaetos (Golden Eagle; Figure 58-Figure 60)
Buteo brachyurus (Short-tailed Hawk; Figure 61)
Buteo lagopus (Rough-legged Hawk; Figure 62-Figure 63)
Buteo lineatus (Red-shouldered Hawk; Figure 64-Figure 65)
Elanoides forficatus (Swallow-tailed Kite; Figure 66)
Elanus leucurus (White-tailed Kite; Figure 67-Figure 68)
Haliaeetus leucocephalus (Bald Eagle; Figure 69)

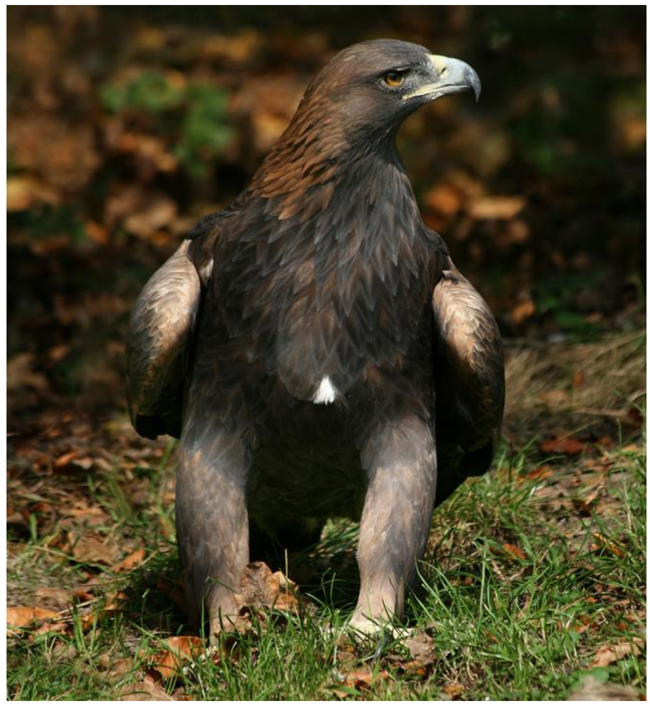

Figure 58. ***Aquila chrysaetos***, Golden Eagle, a species that uses bryophytes in their nests in parts of North America. Photo by Richard Bartz, through Creative Commons.

Figure 59. ***Aquila chrysaetos***, Golden Eagle, nest. Photo by Wildxplorer, through Creative Commons.

Figure 60. ***Aquila chrysaetos***, Golden Eagle, egg and baby on nest. Photo by Johann Jaritz, through Creative Commons.

Figure 61. ***Buteo brachyurus***, Short-tailed Hawk, in flight, a species that uses bryophytes in their nests in parts of North America. Photo by Dario Sanches, through Creative Commons.

Rough-legged Buzzard/Hawk (*Buteo lagopus*)

The Rough-legged Buzzards (***Buteo lagopus***; Figure 62) use mosses to line their nests (Figure 63) (The Hawk Conservancy 1996-2001).

Figure 62. ***Buteo lagopus***, Rough-legged Hawk, a species that lines their nests with mosses. Photo by Walter Siegmund, through Creative Commons.

Figure 63. ***Buteo lagopus***, Rough-legged Buzzard, nest with lining of moss and hatching nestlings. Photo from USFWS, through public domain.

Figure 64. ***Buteo lineatus***, Red-shouldered Hawk, a species that uses bryophytes in their nests in parts of North America. Photo by Mike Baird, through Creative Commons.

Figure 65. ***Buteo lineatus***, Red-tailed Hawk, nest. Photo by Bill Majoros, through Creative Commons.

Figure 66. ***Elanoides forficatus***, Swallow-tailed Kite, in flight. This species uses bryophytes in their nests in parts of North America. Photo by Andrea Westmoreland, through Creative Commons.

Figure 67. ***Elanus leucurus***, White-tailed Kite, carrying nesting material. In parts of North America it includes bryophytes in the nest. Photo by Ken Penicle Jr., through Creative Commons.

Figure 68. ***Elanus leucurus***, White-tailed Kite, on nest. Photo by Maria Teresa Jaramillo, through Creative Commons.

American Bald Eagle (*Haliaeetus leucocephalus*)

It is of some consolation to those who fear extensive loss of mosses that protected birds use mosses for their nests. Even the huge **American Bald Eagle** (***Haliaeetus leucocephalus***; Figure 69) in Alaska uses mosses in old-growth forests to form nests (Figure 69) atop tall spruce trees (Holleman 1997). One can hope that in our efforts to protect our national symbol we will learn to protect those aspects of its habitat that are important to its success. This, hopefully, will protect the mosses.

Figure 69. ***Haliaeetus leucocephalus***, American Bald Eagle, landing on nest. Photo by Murray Foubister, through Creative Commons.

Gruiformes: Cranes, Rails, *etc*

Gruidae – Cranes

Wolf (2009) found one species of **Gruidae** whose members use bryophytes in their nests (Figure 70) in parts of North America of the USA: ***Grus canadensis*** (Sandhill Crane; Figure 71).

Figure 70. ***Grus canadensis***, Sandhill Crane, tending eggs in nest. Photo by Andrea Westmoreland through, Creative Commons.

Figure 71. ***Grus canadensis pratensis***, Sandhill Crane, a species that uses bryophytes in their nests. Photo by Albert Herring, USFWS, through Creative Commons.

Rallidae

Chestnut Forest-Rail (*Rallina rubra*)

The Chestnut Forest-Rail (***Rallina rubra***; see Figure 72) from the Tari Gap, Southern Highlands Province, Papua New Guinea, builds a large, globular nest (Frith & Frith 1990). This domed structure is made of mosses, leaves, and ferns. Its entrance is on the side and the nest sits ~2m above the ground in the crown of the pandanus

palm. Despite the large size of the nest, this rail places only one very large egg in the nest. Although both birds incubate the eggs for their 34-37 days of incubation, the eggs are often left alone long enough that they become cold.

Figure 72. *Rallina fasciata*, Red-legged Crake; the species ***Rallina rubra*** uses mosses in their nests in Papua New Guinea. Photo by J. Wee, through Creative Commons.

Figure 73. ***Charadrius morinellus***, Dotterel male, a species that uses bryophytes in their nests. Photo by Helwig Brunner, through Creative Commons.

Charadriiformes

Charadriidae – Plovers, *etc*

Wolf (2009) found four species of **Charadriidae** that use bryophytes in their nests in parts of North America:

Charadrius semipalmatus (Semipalmated Plover; Figure 76)
Pluvialis apricaria (European Golden-Plover; Figure 77-Figure 78)
Pluvialis dominica (American Golden-Plover; Figure 79-Figure 80)
Pluvialis squatarola (Black-bellied Plover; Figure 81)

Figure 74. ***Racomitrium lanuginosum***, a moss commonly used in nests of the Dotterel. Photo by Niels Klazenga, with permission.

Dotterel (*Charadrius morinellus*)

In Scotland, the rare Dotterel (***Charadrius morinellus***; Figure 73) prefers the *Carex bigelowii*-***Racomitrium lanuginosum*** (Figure 74) moss heath (Welch *et al*. 2005). It feeds largely on beetles, sawflies, and both larvae and adults of ***Tipula montana*** (a common moss inhabitant in its larval stage; see Figure 75) (Galbraith *et al*. 1993). The preferred feeding habitats for these birds are flat or gently sloping ***Racomitrium lanuginosum*** or *Juncus trifidus* heaths or the transition zone between moss heath and montane bog. The most frequently used habitats are those where the montane bogs with best food for juveniles were adjacent to the ***R. lanuginosum*** heaths with the best food for adults.

Figure 75. ***Tipula abdominalis*** larva, a moss dweller in a genus that provides food for the Dotterel. Photo through Creative Commons.

Figure 76. ***Charadrius semipalmatus***, Semi-palmated Plover, a species that uses bryophytes in their nests in parts of North America. Photo by Donna Dewhurst, through public domain.

Figure 77. ***Pluvialis apricaria***, European Golden-Plover. Members of this species use bryophytes in their nests in parts of North America. Photo by Bjørn Christian Tørrissen, through Creative Commons.

Figure 78. ***Pluvialis apricaria***, European Golden-Plover, nest with eggs amid lichens and bryophytes. Photo by Mike Pennington, through Creative Commons.

Figure 79. ***Pluvialis dominica***, American Golden Plover, a species that uses bryophytes in their nests in parts of North America. Photo by O. W. Johnson, USFWS, through public domain.

Figure 80. ***Pluvialis dominica***, American Golden Plover, eggs and nest. Photo by Meegs C, through Creative Commons.

Figure 81. ***Pluvialis squatarola***, Black-bellied Plover, a species that uses bryophytes in their nests in parts of North America. Photo by Peter Wallack, through Creative Commons.

Scolopacidae – Sandpipers, *etc*

Wolf (2009) found eighteen species of **Scolopacidae** that use bryophytes in their nests in parts of North America:

Tringa melanoleuca (Greater Yellowlegs; Figure 82)
Tringa flavipes (Lesser Yellowlegs; Figure 83)
Actitis macularius (Spotted Sandpiper; Figure 84-Figure 85)
Numenius phaeopus (Whimbrel; Figure 86)
Numenius tahitiensis (Bristle-thighed Curlew; Figure 87)
Limosa lapponica (Bar-tailed Godwit; Figure 88)
Arenaria interpres (Ruddy Turnstone; Figure 89-Figure 90)
Aphriza virgata (Surfbird; Figure 91-Figure 92)
Calidris mauri (Western Sandpiper; Figure 93)
Calidris minutilla (Least Sandpiper; Figure 94)
Calidris fuscicollis (White-rumped Sandpiper; Figure 95)
Calidris ptilocnemis (Rock Sandpiper; Figure 96)
Tryngites subruficollis (Buff-breasted Sandpiper; Figure 97)
Limnodromus scolopaceus (Long-billed Dowitcher; Figure 98)
Gallinago gallinago (Common Snipe; Figure 99)
Phalaropus tricolor (Wilson's Phalarope; Figure 100-Figure 101)
Phalaropus lobatus (Red-necked Phalarope; Figure 102-Figure 103)
Phalaropus fulicarius (Red Phalarope; Figure 104)

Figure 82. ***Tringa melanoleuca***, Greater Yellowlegs, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 83. ***Tringa flavipes***, Lesser Yellowlegs chicks. Members of this species use bryophytes in their nests in parts of North America. Photo by S. Kropidlowski, USFWS, through public domain.

Figure 84. ***Actitis macularia***, Spotted Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Mike Baird, through Creative Commons.

Figure 85. ***Actitis macularius***, Spotted Sandpiper, nest with eggs. Photo by Robert A. Hamilton, through Creative Commons.

Figure 86. ***Numenius phaeopus***, Whimbrel, a species that uses bryophytes in their nests in parts of North America. Photo by Valter Jacinto, through Creative Commons.

Figure 87. ***Numenius tahitiensis***, Bristle-thighed Curlew, a species that uses bryophytes in their nests in parts of North America. Photo by Gregory Smith, through Creative Commons.

Figure 88. ***Limosa lapponica***, Bar-tailed Godwit, a species that uses bryophytes in their nests in parts of North America. Photo by Steve Maslowski, USFWS, through public domain.

Figure 89. ***Arenaria interpres***, Ruddy Turnstone, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 90. ***Arenaria interpres***, Ruddy Turnstone, on nest. Photo by Tim Bowman, USFWS, through Creative Commons.

Figure 91. ***Aphriza virgata***, Surfbird, a species that uses bryophytes in their nests in parts of North America. Photo by Marlin Harms, through Creative Commons.

Figure 92. ***Aphriza virgata***, Surfbird, nest with young birds. Photo by Terry Hall, through public domain.

Figure 93. ***Calidris mauri***, Western Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Caleb Slemmons, through Creative Commons.

Figure 94. ***Calidris minutilla***, Least Sandpiper, on shore rock, a species that uses bryophytes in their nests in parts of North America. Photo by Britta, through Creative Commons.

Figure 95. ***Calidris fuscicollis***, White-Rumped Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 96. ***Calidris ptilocnemis***, Rock Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Alan D. Wilson, through Creative Commons.

Figure 97. ***Tryngites subruficollis***, Buff-breasted Sandpiper, a species that uses bryophytes in their nests in parts of North America. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 98. ***Limnodromus scolopaceus***, Long-billed Dowitcher, a species that uses bryophytes in their nests in parts of North America. Photo by Tim Bowman, through Creative Commons.

Figure 99. ***Gallinago gallinago***, Common Snipe, a species that uses bryophytes in their nests in parts of North America. Photo by Alpsdake, through Creative Commons.

Figure 100. ***Phalaropus tricolor***, Wilson's Phalarope, in pond, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Mathson, through Creative Commons.

Figure 101. ***Phalaropus tricolor***, Wilson's Phalarope, male on nest. Photo from NPS, through public domain.

Figure 102. ***Phalaropus lobatus***, Red-necked Phalarope, a species that uses bryophytes in their nests in parts of North America. Photo by Andreas Trepte, through Creative Commons.

Figure 103. ***Phalaropus lobatus***, Red-necked Phalarope on water. Photo by Blake Matheson, through Creative Commons.

Figure 104. ***Phalaropus fulicarius***, Red Phalarope, in shore vegetation, a species that uses bryophytes in their nests in parts of North America. Photo from USFWS, through public domain.

Broad-billed Sandpiper (*Limicola falcinellus*)

The Broad-billed Sandpiper (***Limicola falcinellus***; Figure 105) builds nests in fens dominated by mosses and wet sedges. The nests are built on shallow hummocks, typically in transition zones between vegetation types. Once the baby birds hatch, they are moved from the nest to wetter fen areas nearby. Rae *et al*. (1998) found one nest concealed between two small bryophyte hummocks – one of ***Sphagnum*** *cf*. ***capillifolium*** (Figure 107) and the other possibly ***Aulacomnium*** sp (Figure 108). One was in a *Carex* tussock in a wet fen with 30% ***Hamatocaulis*** *cf* ***vernicosus*** (Figure 109). The nests were often surrounded by a high cover of dark brown bryophytes. The eggs (Figure 106) and chicks were both colored dark chocolate brown, a coloration that Rae and coworkers suggested was an adaptation of **crypsis** (ability to avoid detection) to protect them against predation. Importance of matching color patterns is known in other birds, such as the Stone Curfew (***Burhinus oedicnemus***; Figure 110-Figure 111) (Solis & Lope 1995). These researchers demonstrated that mismatches in coloration between eggs (Figure 112) and the ground in the Stone Curfew increase the predation rate; these birds benefitted by choosing both nest building materials and nest substrate that increased camouflage.

Figure 105. ***Limicola falcinellus***, Broad-billed Sandpiper, a species that nests in mossy wetlands. Photo by Sreedev Puthur, through Creative Commons.

Figure 106. ***Limicola falcinellus***, Broad-billed Sandpiper, eggs that blend with the background of brown mosses. Photo by Klaus Rassinger and Gerhard Cammerer, through Creative Commons.

Figure 107. ***Sphagnum capillifolium***, a species often found in the nesting sites of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Juan Larrain, with permission.

Figure 108. ***Aulacomnium palustre***, a species found in nesting sites of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Kristian Peters through Creative Commons.

Figure 109. ***Hamatocaulis vernicosus***, one of the brown mosses common in the nesting habitat of the Broad-billed Sandpiper (***Limicola falcinellus***). Photo by Michael Lüth, with permission.

Figure 110. ***Burhinus oedicnemus***, Stone Curfew, a species that relies on matching the background colors to the coloration of its eggs. Photo by Artemy Voikhansky, through Creative Commons.

Figure 111. ***Burhinus oedicnemus***, Stone Curlew nesting, a species that relies on matching the background colors to the coloration of its eggs. Photo by Max Pixel, through Creative Commons.

Figure 112. ***Burhinus oedicnemus*** eggs matching their environment. Photo from <www.aerien.ch> through Creative Commons.

Laridae – Skuas, Gulls, Terns, & Skimmers

Wolf (2009) found seventeen species of **Laridae** that use bryophytes in their nests in parts of North America:

Stercorarius parasiticus (Parasitic Jaeger; Figure 114-Figure 115)
Stercorarius pomarinus (Pomarine Jaeger; Figure 116)
Stercorarius longicaudus (Long-tailed Jaeger; Figure 117-Figure 118)
Chroicocephalus philadelphia (Bonaparte's Gull; Figure 119-Figure 120)
Larus canus (Mew Gull; Figure 121-Figure 122)
Larus argentatus (Herring Gull; Figure 123-Figure 124)
Larus thayeri (Thayer's Gull; Figure 125)
Larus glaucoides (Iceland Gull; Figure 126-Figure 127)
Larus hyperboreus (Glaucous Gull; Figure 128-Figure 129)
Larus marinus (Great Black-backed Gull; Figure 130-Figure 131)
Rissa tridactyla (Black-legged Kittiwake; Figure 138)
Rissa brevirostris (Red-legged Kittiwake; Figure 139)
Rhodostethia rosea (Ross's Gull; Figure 140)
Pagophila eburnea (Ivory Gull; Figure 141)
Hydroprogne caspia (Caspian Tern; Figure 142)
Sterna paradisaea (Arctic Tern; Figure 143-Figure 144)
Onychoprion aleuticus (Aleutian Tern; Figure 145)

Stercorarius spp. (Figure 114-Figure 118) prefer mosses, especially ***Polytrichum juniperinum*** (syn. = ***P. alpestre***; Figure 113) (Deeming & Reynolds 2015). Over 60% of their nest material (Figure 115) is mosses.

Figure 113. ***Polytrichum juniperinum,*** a species common in nests of ***Stercorarius*** species. Photo by Vincent de Boer, through Creative Commons.

Figure 114. ***Stercorarius parasiticus***, Arctic Skua/Pomarine Jaeger, a species that uses bryophytes in their nests. Photo by Billy Lindblom, through Creative Commons.

Figure 115. ***Stercorarius parasiticus***, Parasitic Jaeger, nest with eggs and lot of moss. Photo by James K. Lindsey, with permission.

Figure 116. ***Stercorarius pomarinus***, Pomarine Jaeger, a species that uses bryophytes in their nests. Photo by Patrick Coin, through Creative Commons.

Figure 117. ***Stercorarius longicaudus***, Long-tailed Jaeger, nesting. This is a species that uses bryophytes in their nests in parts of North America. Photo by Don Henise, through Creative Commons.

Figure 118. ***Stercorarius longicaudus***, Long-tailed Jaeger, possibly nesting here. Photo through public domain.

Figure 119. ***Chroicocephalus philadelphia***, Bonaparte's Gull, on shore, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 120. ***Chroicocephalus philadelphia***, Bonaparte's Gull, nesting in Alaska. Photo by David Menke, USFWS, through public domain.

Figure 121. ***Larus canus***, Mew Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Kari Pihlaviita, through Creative Commons.

Figure 122. ***Larus canus***, Mew Gull, on nest amid mosses and stones. Photo by John Haslam, through Creative Commons.

Herring/Glaucous Gull Hybrid (*Larus argentatus/hyperboreus*)

Ólafsson (1982) found a pair of gulls, one a Herring Gull (***Larus argentatus***; Figure 123-Figure 124) and the other a Glaucous Gull (***Larus hyperboreus***; Figure 128-Figure 129). Their nest was in a small, collapsed cave. It was constructed almost exclusively of the common moss ***Racomitrium*** (Figure 74). Only one arthropod, a mite, was found among these nest materials.

Figure 123. ***Larus argentatus***, Herring Gull, a species that uses mosses in their nests. Photo by Tony Brierton, through Creative Commons.

Figure 124. ***Larus argentatus***, Herring Gull, nest with mosses under the grass, and eggs. Photo by Finn Rindahl, through Creative Commons.

Figure 125. ***Larus thayeri***, Thayer's Gull, a species that uses mosses in their nests. Photo by Liam O'Brien, through Creative Commons.

Figure 126. ***Larus glaucoides***, Iceland Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Seabamirum, through Creative Commons.

Figure 127. ***Larus glaucoides***, Iceland Gulls, in nesting area. Photo by Seabamirum, through Creative Commons.

Figure 128. ***Larus hyperboreus***, Glaucous Gull, with fledgling. Photo by A. Wieth, through Creative Commons.

Figure 129. ***Larus hyperboreus***, Glaucous Gull, nest with eggs. Photo by Peter Davis, USFWS, through public domain.

Figure 130. ***Larus marinus***, Great Black-backed Gull, a species that uses bryophytes in their nests in parts of North America. Photo by Andreas Trepte, through Creative Commons.

Figure 131. ***Larus marinus***, Great Black-backed Gull, nest and eggs. Photo by Banangraut, through Creative Commons.

Kelp Gull (*Larus dominicus*)

In the Argentine Islands the primary constituent of the Kelp Gull (***Larus dominicus***; Figure 132) nest (Figure 133) is the grass *Deschampsia antarctica* (Figure 134) (Parnikoza *et al*. 2012). The researchers postulated that in making the nests the gulls were responsible for the spread of this grass species on the islands. But the Kelp Gull also uses mosses extensively in its nests. In the Argentine Islands, ***Sanionia uncinata*** (Figure 135) was common and likewise was common in nests. It is particularly suitable because of its pleurocarpous growth form and lack of attachment to its substratum. I would expect that these gulls are similarly able to disperse the mosses.

Figure 132. ***Larus dominicus***, Herring Gull; in the Argentine Islands, this species uses ***Sanionia uncinata*** in their nests. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 133. ***Larus domesticus***, Kelp Gull, nest in Patagonia in a habitat where grasses are readily available, but mosses are not. Photo by Erik Thuesen, through Creative Commons.

Figure 134. *Deschampsia antarctica* (large patch), the grass used for Herring Gull nests in the Argentine Islands. Photo by Sharon Chester, through Creative Commons.

Figure 135. ***Sanionia uncinata***, a moss commonly used in nests of the Kelp Gull. Photo by Hermann Schachner, through Creative Commons.

Lesser Black-Backed Gull (*Larus fuscus*)

When Surtsey arose from the ocean near Iceland in a volcanic explosion, no life existed (Magnússon *et al*. 2008). Slowly plants and flying animals arrived. Among the early bryophytes was the moss ***Racomitrium*** (Figure 74), and this serves as the main nesting (Figure 136) material for the Lesser Black-Backed Gull (***Larus fuscus***; Figure 137) during this austere period.

Figure 136. ***Larus fuscus***, Lesser Black-Backed Gull nest, eggs, & chicks. Photo by Sam Sam, through Creative Commons.

Figure 137. ***Larus fuscus***, Lesser Black-backed Gull, an early Surtsey colonist that uses the moss ***Racomitrium*** for nesting. Photo by Peter Ertl, through Creative Commons.

Figure 138. ***Rissa tridactyla***, Black-legged Kittiwake, on nest. Photo by Sciadopitys, through Creative Commons.

Figure 139. ***Rissa brevirostris***, Red-legged Kittiwakes, at nest. Photo by Art Sowls, through public domain.

Figure 140. ***Rhodostethia rosea***, Ross's Gull, a species that uses bryophytes in their nests in parts of North America. Photo by J. P. Siblet, through Creative Commons.

Figure 141. ***Pagophila eburnea***, Ivory Gull adult, feeding. This species uses bryophytes in their nests in parts of North America. Photo by Alan Vernon, through Creative Commons.

Figure 142. ***Hydroprogne caspia***, Caspian Tern, a species that uses bryophytes in their nests in parts of North America. Photo by B. J. Stacey, through Creative Commons.

Figure 143. ***Sterna paradisaea***, Arctic Tern, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Matheson, through Creative Commons.

Figure 144. ***Sterna paradisaea***, Arctic Tern nest with eggs. Photo by James K. Lindsey, with permission.

Figure 145. ***Onychoprion aleuticus***, Aleutian Tern, a species that uses bryophytes in their nests in parts of North America. Photo by F. Deines, through Creative Commons.

Alcidae – Auks, Murres, & Puffins

Wolf (2009) found four species of **Alcidae** that use bryophytes in their nests in parts of North America:

Brachyramphus marmoratus (Marbled Murrelet; Figure 146-Figure 149)

Brachyramphus brevirostris (Kittlitz's Murrelet; Figure 154-Figure 155)

Ptychoramphus aleuticus (Cassin's Auklet; Figure 156-Figure 157)

Cerorhinca monocerata (Rhinoceros Auklet; Figure 158-Figure 160)

Marbled Murrelet (*Brachyramphus marmoratus*)

When mosses are endangered, few people care, but when a bird shows evidence of disappearance, environmentalists and nature-lovers join forces to protect them. Protecting these birds in pristine habitats can, however, protect mosses as well. The Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146) provides one such story.

Figure 146. ***Brachyramphus marmoratus***, Marbled Murrelet. Photo by Kiliii Yu, through Creative Commons.

Figure 147. ***Brachyramphus marmoratus***, Marbled Murrelet, on mossy nest high in a tree. Photo by Sierra Club, permission pending, site not found.

Figure 148. ***Brachyramphus marmoratus***, Marbled Murrelet chick. Photo by Peter Halasz, through Creative Commons.

Some of our big trees have moss mats that are 30 cm deep on the old firs and Sitka spruce (Krajick 1995a). These mats take centuries to develop and supply

nourishment for canopy-specific birds such as the Marbled Murrelet (***Brachyramphus marmoratus***; Figure 147).

Tompkins (2004) reported that 17 million pounds of mosses had been harvested in 2003 in parts of North America, including Appalachia, with an estimated recovery rate of only 1% per year. The endangered and elusive seabird, the federally threatened Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146), nests (Figure 149) on these moss mats (Figure 147) along the Pacific Coast of the USA (Donahue 1999; Tompkins 2004).

Figure 149. Nest of the Marbled Murrelet (***Brachyramphus marmoratus***) with common moss in the Willamette Valley of the Pacific Northwest, USA. Photo by JeriLynn Peck.

Neville Winchester (in Tompkins 2004) found more than 300 species of mosses in the canopy mats where the Murrelets live. They are so important to the Marbled Murrelet that these birds fly miles inland to build their nests on the mats (Skow 1998; Tompkins 2004). The nest is the size of a baseball and is fashioned into a cup nestled in mosses on a wide tree branch where overhanging branches hide it from its Raven (***Corvus corax***; Figure 150) and Steller's Jay (***Cyanocitta stelleri***; Figure 151) predators (Donahue 1999). The Murrelets prefer trees with high limbs that support wide moss beds. These must be camouflaged by branches to protect the chicks (Figure 148) from predators like jays (Krajick 1995b). Saving the current nesting sites of the birds is essential because these birds return to the same nesting site year after year and rarely change locations (Donahue 1999).

Figure 150. ***Corvus corax***, Raven, a predator of the Marbled Murrelet. Photo by Frank Vassen, through Creative Commons.

Figure 151. ***Cyanocitta stelleri***, Steller's Jay, eating; this is a predator on the Marbled Murrelet. Photo by Rick Leche, through Creative Commons.

The Marbled Murrelet (***Brachyramphus marmoratus***; Figure 146-Figure 148) is distributed from central California to Alaska, living in mature forests of large coastal conifers (Singer *et al*. 1991). Although most of the nests are simple depressions in the moss or lichen mats, others are more constructed. The Marbled Murrelet uses epiphytic mosses (especially ***Isothecium*** spp.; Figure 152) extensively as nesting material (Hamer & Nelson 1995). In California the Marbled Murrelet prefers the moss ***Brachythecium*** (Figure 153) instead (Brian Dykstra, pers. comm. 10 December 2011). Where it is protected, lots of bryophytes are also protected.

Figure 152. ***Isothecium myosuroides***, a species available for nests of the marbled Murrelet. Photo by Adolf Ceska, with permission.

Figure 153. ***Brachythecium rutabulum***, a species available for nests of the marbled Murrelet. Photo by Michael Lüth, with permission.

Figure 154. ***Brachyramphus brevirostris***, Kittlitz's Murrelet, a species that uses bryophytes in their nests in parts of North America. Photo by Ron Niebrugge, through Creative Commons.

Figure 155. ***Brachyramphus brevirostris***, Kittlitz's Murrelet, nest. Photo by USFWS, through public domain.

Figure 156. ***Ptychoramphus aleuticus***, Cassin's Auklet, a species that uses bryophytes in their nests in parts of North America. Photo by Blake Matheson, through Creative Commons.

Figure 157. ***Ptychoramphus aleuticus***, Cassin's Auklet, on nest. Photo by L. Lauber, USFWS, public domain.

Figure 158. ***Cerorhinca monocerata***, Rhinoceros Auklet, a species that uses bryophytes in their nests in parts of North America. Photo by Dick Daniels, through Creative Commons.

Figure 159. ***Cerorhinca monocerata***, Rhinoceros Auklet, nest burrows. Photo by through Creative Commons.

Figure 160. ***Cerorhinca monocerata***, Rhinoceros Auklet, nest burrow and female. Photo by NOAA, through public domain.

Summary

The use of bryophytes in nests is much more common among the **Passeriformes** than among the non-**Passeriformes**. The latter are mostly ground-nesting birds. Some build their nests on the mosses and others gather bryophytes to include in their nests. In the Arctic and Antarctic, use of bryophytes in nest construction is common due to the limited vegetation available. There, even water birds commonly use bryophytes.

Burrowing birds may use bryophytes as liners in the burrows, sometimes providing a nest for rodents that move in later. Hummingbirds often use mosses and lichens on the outsides of nests, presumably as camouflage. The Picaflor Rubi is one of the birds that can make its entire nest with bryophytes.

Some birds require mossy wetlands nearby their nesting sites because those wetland sites provide food needed for the young.

Protection of birds such as the Marbled Murrelet, a species that flies inland to mossy habitats to nest, may effectively protect the bryophytes as well.

Acknowledgments

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CHAPTER 16-5
BIRD NESTS – NON-PASSERIFORMES, PART 2

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CHAPTER 16-5
BIRD NESTS – NON-PASSERIFORMES, PART 2

Figure 1. Bird's nest with living moss in Malaysia rain forest at 110 m alt. Photo courtesy of Tamas Pocs.

Columbiformes: Pigeons & Doves

Columbidae – Pigeons & Doves

Wolf (2009) found only one species of **Columbidae** that uses bryophytes in their nests in parts of North America: ***Patagioenas fasciata*** (Band-Tailed Pigeon; Figure 2-Figure 3).

Figure 2. ***Patagioenas fasciata***, Band-Tailed Pigeon, the only member of **Columbidae** that uses mosses in their nests in parts of North America. Photo by Gary Kramer, through public domain.

Figure 3. ***Patagioenas fasciata***, Band-tailed Pigeon, on nest. Photo by Cgates326, through Creative Commons.

Cuculiformes: Cuckoos & Relatives

Cuculidae – Typical Cuckoos

Wolf (2009) found one species of **Cuculidae** that uses bryophytes in their nests in parts of North America: ***Coccyzus americanus*** (Yellow-billed Cuckoo; Figure 4). Unlike the European Cuckoo, the Yellow-billed Cuckoo usually builds its own nest, only occasionally laying eggs in the nest of another species (Wikipedia 2017).

Figure 4. ***Coccyzus americanus***, Yellow-billed Cuckoo, a bird that uses mosses in nests. Photo by Factumquintus, through Creative Commons.

Strigiformes: Owls

Strigidae – Typical Owls

Wolf (2009) found five species of **Strigidae** that use bryophytes in their nests in parts of North America:

Bubo virginianus (Great Horned Owl; Figure 5-Figure 6)
Bubo scandiacus (Snowy Owl; Figure 7)
Glaucidium gnoma (Northern Pygmy Owl; Figure 8)
Strix nebulosa (Great Gray Owl; Figure 9-Figure 10)
Aegolius acadicus (Northern Saw-whet Owl; Figure 11-Figure 12)

Figure 5. ***Bubo virginianus***, Great Horned Owls, in nest where mosses are often used. Photo by John Kees, through Creative Commons.

Figure 6. ***Bubo virginianus***, Great Horned Owl chicks. Photo by G. M. Stolz, through Creative Commons.

Snowy Owl (*Bubo scandiacus*)

Snowy Owls (***Bubo scandiacus***; Figure 7) use mosses as nest liners (Giannetta 2000).

Figure 7. ***Bubo scandiacus***, Snowy Owl. Members of this species use mosses to line their nests. Photo by David Syzdek, through Creative Commons.

Figure 8. ***Glaucidium gnoma***, Northern Pygmy Owl, a species that uses bryophytes in their nests in parts of North America. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 9. ***Strix nebulosa***, Northern Pygmy Owl. Members of this species use bryophytes in their nests in parts of North America. Photo by jok2000, through Creative Commons.

Figure 10. ***Strix nebulosa***, Northern Pygmy Owl, on nest. Photo by Kuva, through Creative Commons.

Figure 11. ***Aegolius acadicus***, Northern Saw-whet Owl. Members of this species use bryophytes in their nests in parts of North America. Photo by Robert L. Curtis, through Creative Commons.

Figure 12. ***Aegolius acadicus***, Northern Saw-whet Owl, young. Photo by Kathy and Sam, through Creative Commons.

Burrowing Owls (*Athene cunicularia*)

Thomsen (1971) reminds us that Burrowing Owls (***Athene cunicularia***; Figure 13-Figure 14) decorate their burrows (Figure 15) with mosses, among other things. The burrowing owl often does not make its own burrow, but rather uses the underground village of a marmot or prairie dog (Rennie 1857). At St. Domingo the owl digs a burrow 70 cm deep and deposits its eggs on a bed of moss.

Figure 13. ***Athene cunicularia***, Burrowing Owls, ground-nesting birds that use burrows. Photo by Travelwayoflife, through Creative Commons.

Figure 14. ***Athene cunicularia hypugaea***, Burrowing Owl. Members of this species decorate their burrows with mosses. Photo by Teddy Llovet, through Creative Commons.

Figure 15. ***Athene cunicularia***, Burrowing Owl, nest hole. Photo by USFWS, through Creative Commons.

Caprimulgiformes: Goatsuckers & Relatives

Caprimulgidae – Goatsuckers

Wolf (2009) found one species (***Chordeiles minor*** – Common Nighthawk; Figure 16) of **Caprimulgidae** that uses bryophytes in their nests (Figure 17-Figure 18) in parts of North America.

Figure 16. ***Chordeiles minor***, Common Nighthawk, on a bed of mosses. Photo by Gavin Keefe Schaefer, through Creative Commons.

Figure 17. ***Chordeiles minor***, Common Nighthawk, eggs in nest of mosses. Photo by Mike Allen, through Creative Commons.

Figure 18. ***Chordeiles minor***, Common Nighthawk, hatchlings in nest. Photo by Mike Allen, through Creative Commons.

Apodiformes: Swifts & Hummingbirds

Apodidae – Swifts

Wolf (2009) found only two members of the **Apodidae** that use bryophytes in their nests in parts of North America:

Cypseloides niger (Black Swift; Figure 19-Figure 20)
Aeronautes saxatalis (White-throated Swift; Figure 21-Figure 22)

Figure 19. ***Cypseloides niger***, Black Swift, adult on mossy nest. Photo by Terry Gray, through Creative Commons.

Figure 20. ***Cypseloides niger***, Black Swift, nest. Photo through Creative Commons.

Figure 21. ***Aeronautes saxatalis***, White-throated Swift, at cliff. Members of this species use bryophytes in their nests in parts of North America. Photo by Richard Crossley, through Creative Commons.

Figure 22. ***Aeronautes saxatalis***, White-throated Swift, in flight. Photo by Michael Woodruff, through Creative Commons.

Glossy Swiftlets (*Collocalia*)

Medway (1966) found that at least some of the European swiftlets (***Collocalia*** and ***Aerodramus***) build bracket-shaped nests of mosses and other bryophytes that are bound together. The Glossy Swiftlets (***Collocalia esculenta***; Figure 23) include bryophytes in their nests, along with horse-hair fungi and palm fibers (Sick 1957; Medway 1962).

Figure 23. ***Collocalia esculenta***, Glossy Swiftlet, a species whose members build nests made entirely of bryophytes in the Philippines. Photo through Creative Commons.

In the Philippines, Tan *et al*. (1982) discovered three nests of ***Collocalia esculenta*** (Glossy Swiftlet; Figure 23) that contained only bryophytes. One was a nest of a single species of the leafy liverwort ***Frullania*** (Figure 24). One nest was constructed of stems of the tiny leafy liverwort ***Mastigolejeunea*** sp. (85%) with scattered mosses [***Papillaria fuscescens*** (see Figure 25), ***Meteorium*** (Figure 26), ***Acroporium*** (Figure 27)]. The third nest had a large compartment of only the leafy liverwort ***Frullania*** and a small one of the mosses ***Papillaria fuscescens*** and ***Aerobryidium*** *cf*. ***filamentosum*** (Figure 28). In all three nests the bryophytes were neatly glued together with saliva from the birds. Some of the bryophytes continued to grow

in the nests, but the shoots were attenuated and the leaf shapes abnormal. Of the mosses, only pleurocarpous species were used, and all the bryophytes were epiphytic high in the canopy of a dipterocarp forest. Furthermore, the bryophytes used were only common close to the summit of the mossy forest. Abundant ground species were completely ignored.

Figure 24. ***Frullania*** sp., a leafy liverwort used to make nests of ***Collocalia esculenta*** in the Philippines. Photo by Li Zhang, with permission.

Figure 25. ***Papillaria***, a genus used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Michael Lüth, with permission.

Figure 26. ***Meteorium***, a genus used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Janice Glime.

Figure 27. ***Acroporium pungens***, member of a genus used in nests by ***Collocalia esculenta*** in the Philippines. Photo by Michael Lüth, with permission.

Figure 28. ***Aerobryidium filamentosum***, a moss species used in nests of ***Collocalia esculenta*** in the Philippines. Photo by Taiwan Liverworts Color Illustrations, through Creative Commons.

Unlike most birds I have seen, ***Collocalia esculenta*** carry their nesting materials with their feet, flying at the tufts of epiphytes, grabbing with their feet and leaning back (Medway 1962). They beat their wings and tug at the bryophyte fronds. Carrying the mosses in their feet makes

the birds tail-heavy and flying is laborious. Fragments are often dropped, and long strands may hang from the nest until the birds are able to weave them into the nest. The mosses are held in place by gumming them to the underlying debris or cave wall. Nests are often deep in caves. This species is able to echo-navigate, so total darkness in the cave is no hindrance.

Mossy-nest Swiftlet (*Aerodramus salangana*)

The moss use by the Mossy-nest Swiftlet (***Aerodramus salangana***; Figure 29) is obvious by its name. The Mossy-nest Swiftlet in Malaysia builds a rounded nest made of plant material (Figure 30) (Medway 1962). Among three nests examined by Medway, the components were *Selaginella* sp. (a lycophyte; Figure 31) 75%, ***Piloecium pseudorufescens 5%***, ***Piloecium pseudorufescens*** 90%, ***Octoblepharum albidum*** (Figure 32) a little; ***Neckeropsis lepineana*** (Figure 33) 80%, ***Pinnatella kuehliana*** 10%, These are all epiphytic mosses except *Selaginella*, a genus that often resembles a moss. ***Octoblepharum*** is the only acrocarpous genus.

Figure 29. ***Aerodramus salangana***, Mossy-nest Swiftlet, showing its cave habitat. Photo by Bernard Dupont, through Creative Commons.

Figure 30. ***Aerodramus salangana natunae***, Mossy-nest Swiftlet nest and nestlings, showing mosses in nest. Photo by Bernard Dupont, through Creative Commons.

Figure 31. ***Selaginella willdenowii***, a moss-like lycophyte in a genus used in nests of the Mossy-nest Swiftlet in Malaysia. Photo copyright Patrick Blanc, permission implied.

Figure 32. ***Octoblepharum albidum***, a moss included in the nests of the Mossy-nest Swiftlet (***Aerodramus salangana***). Photo by Bramadi Arya, through Creative Commons.

Figure 33. ***Neckeropsis lepineana***, a moss included in the nests of the Mossy-nest Swiftlet (***Aerodramus salangana***). Photo by Colin Meurk, through Creative Commons.

Mascarene Swiftlet (*Aerodramus francicus*)

Billiet and Jadin (1979, Jadin & Billiet 1979) reported that the **Mascarene Swiftlet** (***Aerodramus francicus***; Figure 34) uses mosses, liverworts, and lichens glued together with saliva.

Figure 34. ***Aerodramus francicus***, Mascarene Swiftlet, a bird that uses bryophytes in its nests. Photo by Eliane Küpfer, through Creative Commons.

Philippine Swiftlet (*Aerodramus vanikorensis amelis*)

The Philippine Swiftlets (***Aerodramus vanikorensis amelis***; Figure 35) use both lichens and mosses in their nests (Tan *et al*. 1982).

Figure 35. ***Aerodramus vanikorensis amelis***, Philippine Swiftlet, sitting on its mossy nest. Photo by Guy Poisson, with permission.

Trochilidae – Hummingbirds

Wolf (2009) found eight members of the **Trochilidae** that use bryophytes in their nests in parts of North America:

Hylocharis leucotis (White-eared Hummingbird; Figure 36)
Eugenes fulgens (Magnificent Hummingbird; Figure 37)
Archilochus alexandri (Black-chinned Hummingbird; Figure 38-Figure 40)
Calypte anna (Anna's Hummingbird; Figure 43-Figure 46)
Stellula calliope (Calliope Hummingbird; Figure 47-Figure 48)
Selasphorus platycercus (Broad-tailed Hummingbird; Figure 49-Figure 51)
Selasphorus rufus (Rufous Hummingbird; Figure 52-Figure 53)
Selasphorus sasin (Allen's Hummingbird; Figure 54-Figure 55)

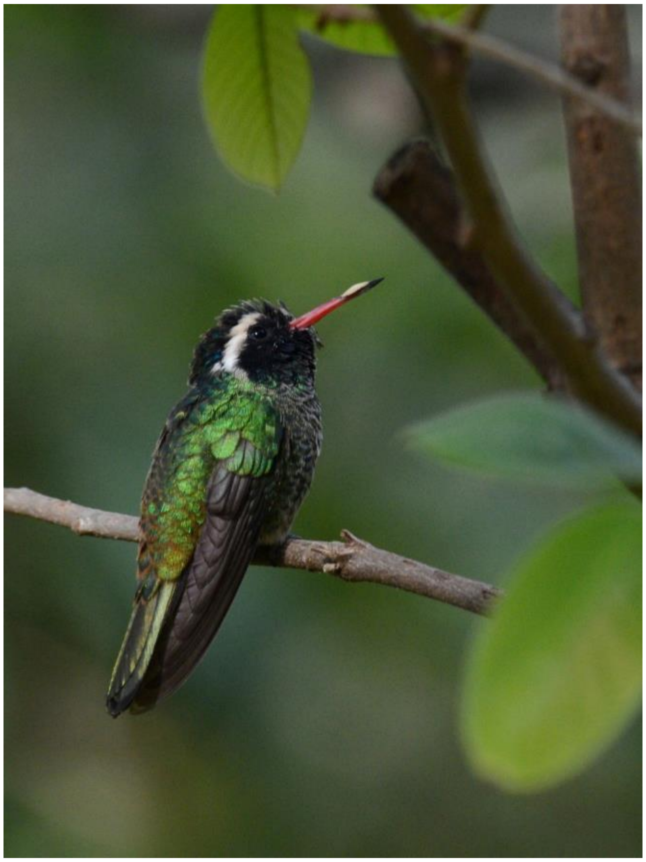

Figure 36. ***Hylocharis leucotis***, White-eared Hummingbird, a bird that uses bryophytes in its nests in parts of North America. Photo by Amado Demesa, through Creative Commons.

Figure 37. ***Eugenes fulgens***, Magnificent Hummingbird, a bird that uses bryophytes in its nests in parts of North America. Photo by Dmitry Mozzherin, through Creative Commons.

Figure 38. ***Archilochus alexandri***, Black-chinned Hummingbird, a bird that uses bryophytes in its nests. Photo by Greg Lasley, through Creative Commons.

Figure 39. ***Archilochus alexandri***, Black-chinned Hummingbird. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 40. ***Archilochus alexandri***, Black-chinned Hummingbird, nest. Photo by Benedict Gagliardi, through Creative Commons.

Ruby-throated Hummingbird (*Archilochus colubris*)

The Ruby-throated Hummingbird (***Archilochus colubris***; Figure 41) builds a tiny nest (Figure 42) to house two pea-sized eggs (Bell 2001). These nests are located on thin branches of understory trees. They consist of an inner cup lined with fine plant down and camouflaged on the outside with small pieces of mosses and lichens. These are held together with spider webs, which are also used to affix the nest to the branch.

Figure 41. ***Archilochus colubris***, Ruby-throated Hummingbird. Members of this species use mosses and lichens on the outsides of their nests, creating camouflage. Photo by Matt Tillett, through Creative Commons.

Figure 42. ***Archilochus colubris***, Ruby-throated Hummingbird, on nest. Photo by Choess, through Creative Commons.

Figure 43. ***Calypte anna***, Anna's Hummingbird. Members of this species use bryophytes in their nests. Photo by Don Loarie, through Creative Commons.

Figure 44. ***Calypte anna***, Anna's Hummingbird, head. Photo by James Maughn, through Creative Commons.

Figure 45. ***Calypte anna***, Anna's Hummingbird, nest with mosses. Photo by Steve Berardi, through Creative Commons.

Figure 46. ***Calypte anna***, Anna's Hummingbird, nest with mostly lichens on the outside, but with a few bryophytes mixed in. Photo by Emily Hoyer, through Creative Commons.

Figure 47. ***Stellula calliope***, Calliope Hummingbird. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 48. ***Stellula calliope***, Calliope Hummingbird, feeding young in nest. Photo by Katia Schulz, through Creative Commons.

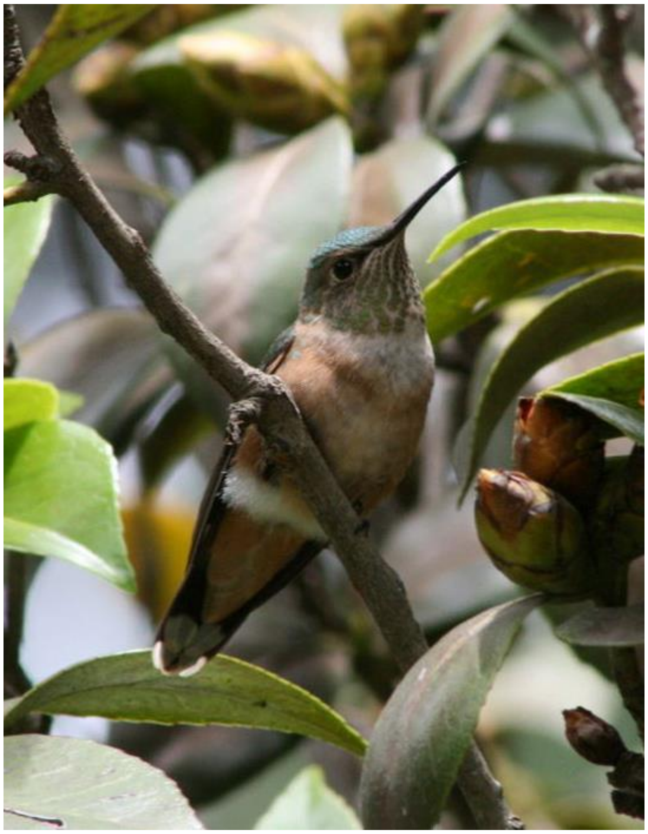

Figure 49. ***Selasphorus platycercus***, Broad-tailed Hummingbird. Members of this species use bryophytes in their nests. Photo by Alfonso Gutiérrez Aldana, through Creative Commons.

Figure 50. ***Selasphorus platycercus***, Broad-tailed Hummingbird. Photo by Michele Lynn Reynolds, through Creative Commons.

Figure 51. ***Selasphorus platycercus***, Broad-tailed Hummingbird, feeding young in nest. Photo by Bill Ratcliff, NPS, through public domain.

Rufous Hummingbird (*Selasphorus rufus*)

The Rufous Hummingbird (***Selasphorus rufus***; Figure 52) breeds in open areas and forest edges of western North America (Wikipedia 2011). It nests the farthest north of any hummingbird and the female builds its nest (Figure 53) in a shrub or conifer where it is protected. The male aggressively defends this tiny nest. The nests are built in lower branches in spring, benefitting from the temperature amelioration by the canopy. In summer the nests are built higher in the tree (Horvath 1964).

Figure 52. ***Selasphorus rufus***, Rufous Hummingbird male. Photo by Rick Leche, through Creative Commons.

Figure 53. ***Selasphorus rufus***, Rufous Hummingbird, female on nest with mosses and lichens on the exterior of the nest. Photo by Rick Leche, through Creative Commons.

Figure 54. ***Selasphorus sasin***, Allen's Hummingbird. Members of this species use bryophytes in their nests. Photo by Jesse Rorabaugh, through Creative Commons.

Figure 55. ***Selasphorus sasin***, Allen's Hummingbird, on nest that has a few bryophytes. Photo by Asicnewbie, through Creative Commons.

Picaflor Rubí (*Sephanoides sephaniodes*)

The Picaflor Rubí, also known as the Green-backed Firecrown or Picaflor Chico, is a South American hummingbird named ***Sephanoides sephaniodes*** (Figure 57). This tiny bird uses mosses and lichens for its nest (Figure 56), including the moss ***Ancistrodes genuflexa*** (Figure 56-Figure 58) (Torres-Dowdall *et al*. 2007). It seems it prefers this to other pendent mosses in the same family, such as ***Weymouthia cochlearifolia*** (Figure 59) and ***W. mollis*** (Figure 60). On the other hand, in Chile, the Picaflor Rubi uses the tree fern ***Lophosoria quadripinnata*** (Figure 61) in all of the "garments" (materials located inside nest), providing a soft texture and a brown color to the nests (Osorio Zúñiga 2012). The pendent mosses ***Weymouthia cochlearifolia***, ***W. mollis***, and ***Ancistrodes genuflexa*** occur on the outside as 16.6, 26.6, and 100% of the nests, respectively. Among these latter species 20, 37.5 and 40% produced reproductive structures in the nests (Figure 62). In older nests, reproductive structures still occurred on ***Eriodon conostomus*** (Figure 63), ***Ptychomnion ptychocarpon***, and ***Dicranoloma robustum*** (Figure 64). Most of these mosses were taken at heights of 10-18 m from the ground and were not the most abundant species found there. Thus, there is selectivity of the bryophytes used for nesting material.

Figure 56. A nest of the Picaflor Chico (***Sephanoides sephaniodes***), with the bird's tail barely visible, for which the nesting material is primarily ***Ancistrodes genuflexa***. Photo courtesy of Felipe Osorio Zúñiga.

Figure 57. ***Sephanoides sephaniodes***. Members of this species often build their nests almost entirely of mosses. Photo by Greg Lasley, through Creative Commons.

Figure 58. The pendent moss ***Ancistrodes genuflexa*** in Chile, a moss used in the nests of ***Sephanoides sephaniodes***, known there as the Picaflor Chico. Photo courtesy of Felipe Osorio Zúñiga.

Figure 59. ***Weymouthia cochlearifolia***, a pendent moss used in the nests of ***Sephanoides sephaniodes***. Photo by Juan Larrain, through Creative Commons.

Figure 60. ***Weymouthia mollis***, a pendent moss used in the nests of ***Sephanoides sephaniodes***. Photo by Juan Larrain, through Creative Commons.

Figure 61. ***Lophosoria quadripinnata***, a fern used in the nests of ***Sephanoides sephaniodes***. Photo by Franz Xaver, through Creative Commons.

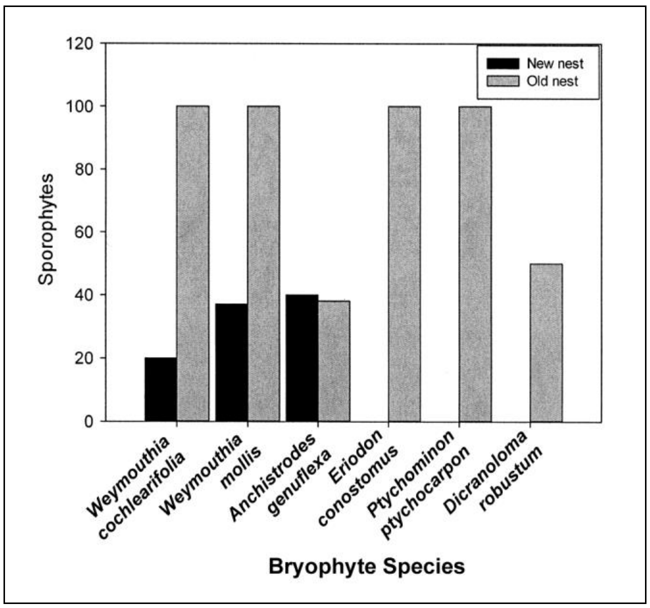

Figure 62. Number of sporophytes vs bryophyte species and nest age of the Picaflor Chico (***Sephanoides sephaniodes***) in Chile. Redrawn from Osorio Zúñiga 2012.

Figure 63. ***Eriodon conostomus*** with capsules, a moss that produces capsules in older nests of Picaflor Rubi. Photo by Juan Larrain, through Creative Commons.

Figure 64. ***Dicranoloma robustum*** with capsules, a moss that produces capsules in older nests of Picaflor Rubi. Photo by Juan Larrain, with permission.

In Patagonia, Argentina, ***Sephanoides sephaniodes*** (Figure 57) is known as the Green-backed Firecrown (Calvelo *et al*. 2014). This species, and the White-sided Hillstar, ***Oreotrochilus leucopleurus*** (Figure 65), likewise used primarily mosses in their nests, but they both interestingly selected mosses with **falcate** (sickle-shaped – see leaves of ***Dicranoloma***; Figure 64) leaves. These were entangled with spider webs and concealed on the outside with spider cocoons, leprose lichens, feathers, and hairs.

Figure 65. ***Oreotrochilus leucopleurus***, White-sided Hillstar. Members of this species like falcate mosses for their nests. Photo by Pablo Caceres Contreras, through Creative Commons.

Osorio-Zuñiga *et al*. (2014) determined that ***Sephanoides sephaniodes*** (Figure 57) was selective in its nesting materials. The bulk of the nest was made from the fern ***Lophosoria quadripinnata*** (Figure 61) (and the moss ***Ancistrodes genuflexa*** – Figure 58). Six other mosses were included in lesser quantities, although 19 species were

available in the area. The birds were further selective in collecting higher densities of reproductive mosses than that represented in the environment. These reproductive structures remained for more than a year, suggesting that this nest-building behavior could be an effective dispersal mechanism. By placing the sporophytes at a greater height, the birds enable dispersal to a greater distance.

More recently, Fontúrbel *et al*. (2020) reported that ***Ancistrodes genuflexa*** occurs in 100% of the nests, makes up 97% of the moss biomass in the nests, but is only 0.1% of the total moss biomass in the forest. The other two mosses that are present in any regularity are ***Weymouthia mollis*** (in 27% of nests) and ***W. cochlearifolia*** (in 17% of nests). These two species provide only 3% of the moss biomass in the nests, but comprise 94% of the moss biomass in the forest. Knowing that mosses often have antibiotic properties, reasoned that this attribute might account for the selection. Hence, the researchers tested the three primary nest components for their antibacterial agents. In ***A. genuflexa***, they found 14 compounds. Of these, five are known to have antibacterial properties, one has antifungal properties, and one repels insects (Asakawa *et al*. 2013)! Although the two ***Weymouthia*** species are known to have antimicrobial properties, neither species was effective against the five common bacteria tested. Furthermore, when the mosses were kept in the lab at 4ºC, both ***Weymouthia*** species were attacked by fungi and rotted after six months, whereas the ***A. genuflexa*** samples were unharmed for a year. Since ***Sephanoides sephaniodes*** may reuse its nest for several years, it is likely that it experiences greater survival when it uses ***A. genuflexa*** at its primary nesting material. As Fontúrbel and coworkers titled their article, "Mamma knows best."

The hummingbirds commonly use mosses and lichens in their nests, so it is not surprising that the endemic Juan Fernandez Firecrown (***Sephanoides fernandensis***; Figure 66-Figure 67) makes its nest almost entirely of mosses (Figure 68) (Jaime Jiminez, pers. comm. 19 May 2020).

Figure 66. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Figure 67. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Figure 68. ***Sephanoides fernandensis*** (Juan Fernandez Firecrown) female on nest in Juan Fernandez area. Photo courtesy of Jaime Jiminez.

Trogoniformes

Trogonidae – Trogons

Wolf (2009) found only one species of **Tyrannidae** whose members use bryophytes in nests in parts of North America: ***Trogon elegans*** (Elegant Trogon; Figure 69).

Figure 69. ***Trogon elegans***, Elegant Trogon, a species that uses bryophytes in nests in parts of North America. Photo by Dominic Sherony, through Creative Commons.

Summary

Burrowing Owls may use bryophytes as liners in the burrows, sometimes providing a nest for rodents that move in later. Some swiftlets make extensive use of mosses in their nests. Hummingbirds often use mosses and lichens on the outsides of nests, presumably as camouflage. The Picaflor Rubi is one of the hummingbirds that can make its entire nest with bryophytes, selecting ***Ancistrodes genuflexa*** in much greater proportion than its presence in the forest, apparently for its antibiotic properties.

Pleurocarpous bryophytes are the most common in nests, and tree-nesting tropical birds typically use epiphytic bryophytes, including pendent species.

Acknowledgments

Thank you to Brian Dykstra for sending me the wonderful thesis on birds and epiphytes by Adrian Wolf, as well as other references and personal observations. David Dumond shared the references he got from Bryonetters. Filipe Osorio Zúñiga provided me with information and images for the Picaflor Chico. Jaime Jiminez provided me with images and natural history information on ***Sephanoides fernandensis***. Thank you to these and all the photographers who made their images available to me online or gave me permission.

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CHAPTER 16-6
BIRD NESTS – PASSERIFORMES, PART 1

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CHAPTER 16-6
BIRD NESTS – PASSERIFORMES, PART 1

Figure 1. Moss nest from the Pacific Northwest, USA. The bryophytes include ***Isothecium*** and ***Neckera***. Photo courtesy of Jerilyn Peck.

Passeriformes: Perching Birds

This is a large order (>5000 species) and comprises most of the birds that use bryophytes in their nests. But then, it also includes more than half the bird species in the world (Wikipedia 2017). The order is distinguished by having three toes pointing forward and one pointing back, permitting these to be perching birds. Passerines also are **altricial** (hatched or born in undeveloped state and requiring care and feeding by parents).

Richardson (1981) reports that a quarter of the bird species breeding in Great Britain use bryophytes in the construction of their nests. Hansell (2000) likewise reports that numerous small to medium-sized bird species use bryophytes.

Large passerine birds tend to build larger nests relative to their body size when compared to small birds (Slagsvold 1989). The depth of the inner nest cup size of these birds does not relate to the size of the bird. Birds that nest off the ground in open nests have a narrow nest cup, but those with a domed nest or which build in a cavity have a broad nest cup. Birds in exposed nests are less likely to survive than those reared in nest cavities (Nice 1937, 1957). There seem to be no data on the success of birds reared in nests made totally of mosses. Mosses and lichens alter the nest cup size, with the inner nest cup being narrower when more are used (Slagsvold 1989). Use of mosses and lichens also depends on season, with those birds nesting early in the breeding season using significantly more mosses and lichens than are used in later nests.

In coniferous forests, bryophytes are often abundant. Several species of birds that breed there build nests exclusively of bryophytes. These include the Winter Wren (see below; Hejl *et al*. 2002), Marbled Murrelet (see Chapter 16-7; Nelson 1997), and Golden-crowned Kinglet (see Chapter 16-7; Ingold & Galati 1997). In addition, Sakai (1988) described a Hammond Flycatcher nest (see below) made with two epiphytic lichens and five bryophytes, including the epiphytic moss ***Isothecium*** sp. (Figure 11) and liverwort, ***Porella navicularis*** (Figure 17).

Tyrannidae – Tyrant Flycatchers

Wolf (2009) found fifteen species of **Tyrannidae** that use bryophytes in their nests in North America:

Contopus sordidulus (Western Wood-Pewee; Figure 2)
Empidonax flaviventris (Yellow-bellied Flycatcher; Figure 4)
Empidonax alnorum (Alder Flycatcher; Figure 5)
Empidonax minimus (Least Flycatcher; Figure 6)
Empidonax difficilis (Pacific-slope Flycatcher; Figure 7-Figure 8)
Empidonax hammondii (Hammond's Flycatcher; Figure 13)
Empidonax occidentalis (Cordilleran Flycatcher; Figure 18)
Sayornis nigricans (Black Phoebe; Figure 19)
Sayornis phoebe (Eastern Phoebe; Figure 20-Figure 21)
Sayornis saya (Say's Phoebe; Figure 26-Figure 27)
Pitangus sulphuratus (Great Kiskadee; Figure 28)
Tyrannus melancholicus (Tropical Kingbird; Figure 31)
Tyrannus couchii (Couch's Kingbird; Figure 32)
Tyrannus forficatus (Scissor-tailed Flycatcher; Figure 33)
Pachyramphus aglaiae (Rose-throated Becard; Figure 37)

Figure 2. ***Contopus sordidulus***, Western Wood Pewee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Olive-sided Flycatcher (*Contopus cooperi*)

The Olive-sided Flycatchers (***Contopus cooperi***; Figure 3) typically hide their nests in a cluster of needles and twigs at distal ends of horizontal conifer branches (Johnsgard 2009). These may occur anywhere from 5-13 m above the ground. They use twigs, lichens, mosses, and needles to construct a cup ~12-15 cm in diameter.

Figure 3. ***Contopus cooperi***, Olive-sided Flycatcher. Members of this species often include mosses in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Yellow-bellied Flycatcher (*Empidonax flaviventris*)

In the eastern United States, Yellow-bellied Flycatcher (***Empidonax flaviventris***; Figure 4) nests close to mature stands of lowland coniferous forest (Harrison 1975; Hawrot & Niemi 1996). These forests often have a well-developed layer of mosses and these mosses appear to be necessary for the bird's nesting. The Yellow-bellied Flycatcher nests on the ground in a layer of mosses.

Figure 4. ***Empidonax flaviventris***, Yellow-bellied Flycatcher. This species builds nests on a bed of mosses on the ground. Photo by Cephas, through Creative Commons.

Figure 5. ***Empidonax alnorum***, Alder Flycatcher. Members of this species often include mosses in their nests. Photo by Cephas, through Creative Common.

Figure 6. ***Empidonax minimus***, Least Flycatcher. Members of this species often include mosses in their nests. Photo by MDF, through Creative Commons.

Pacific-slope Flycatcher (*Empidonax difficilis*)

The Pacific-slope Flycatcher (***Empidonax difficilis***; Figure 7-Figure 8) typically builds nests on ledges or crevices of canyon walls (Johnsgard 2009). These are often concealed by mosses or ferns. When the nest is built on trees, they are supported from below and from the rear, occurring in a crotch or on a limb that projects far from the main trunk. They contain a variety of materials, frequently including mosses (Figure 8-Figure 9).

Figure 7. ***Empidonax difficilis***, Pacific-slope Flycatcher, a species that uses ***Isothecium*** in their nests in Douglas fir forests of the Pacific Northwest, USA. Photo by Ron Knight, through Creative Commons.

Figure 8. ***Empidonax difficilis***, Pacific-slope Flycatcher mossy nest with eggs. Photo from USFWS, through Creative Commons.

Figure 9. ***Empidonax difficilis***, Pacific-slope Flycatcher, nest with mosses and young bird. Photo by Don Loarie, through Creative Commons.

In the Pacific Northwest, USA, Wolf (2009) found a nest of the Pacific-slope Flycatcher (Figure 8) on a fractured piece of bark on the tree bole of ***Pseudotsuga menziesii*** (Figure 10) at ~4 m above the ground. The bird had woven strands of the moss ***Isothecium*** (Figure 11) into the rim of the nest and decorated the exterior with fragments of the lichen ***Sphaerophorus globosus*** (Figure 12). The ***Isothecium*** had been relocated from elsewhere in the forest understory.

Figure 10. ***Pseudotsuga menziesii*** bark where Pacific-slope Flycatchers (***Empidonax difficilis***) build their nests in crevices. Photo by Walter Siegmund, through Creative Commons

Figure 11. ***Isothecium myosuroides***, representing a genus among those used in nests of the Pacific-slope Flycatcher (***Empidonax difficilis***). Photo by Hermann Schachner, through Creative Commons.

Figure 12. ***Sphaerophorus globosus***, one of the lichen materials used in nests of the Pacific-slope Flycatcher (***Empidonax difficilis***). Photo by Einar Timdal, through Creative Commons.

Hammond's Flycatcher (*Empidonax hammondii*)

The Hammond's Flycatcher (***Empidonax hammondii***; Figure 13) has a nest that is distinctly different from that of the Pacific Slope Flycatcher (***Empidonax difficilis***; Figure 7-Figure 9) (Sakai 1988). The Hammond's Flycatcher nest is taller, more tightly woven, and mimics the surrounding substrate. The outer bowl of the only retrieved nest was made with mostly white scale lichens, mosses ***Dendroalsia abietina*** (Figure 14), ***Homalothecium nuttallii*** (Figure 15), ***Isothecium*** sp. (Figure 11), ***Alsia*** sp. (Figure 16), and the leafy liverwort ***Porella navicularis*** (Figure 17). By comparison, in the 22 Pacific-slope Flycatcher nests, the material was mostly mosses. They often lacked the camouflage effect because they used the same materials on all substrates. The nests were held together with spider webs that were also used to secure the nests to the substrate.

Figure 13. ***Empidonax hammondii***, Hammond's Flycatcher. Members of this species often include mosses in their nests. Photo by Pablo Leautaud, through Creative Commons.

Figure 14. ***Dendroalsia abietina***, a nest component of the Hammond's Flycatcher in the Pacific Northwest. Photo by James Maughn, through Creative Commons.

Figure 15. ***Homalothecium nuttallii***, a species used in nests of the Hammond's Flycatcher in the Pacific Northwest. Photo by Doug Murphy, through Creative Commons.

Figure 16. ***Alsia californica***, member of a genus used in nests of the Hammond's Flycatcher in parts of North America. Photo by John Game, through Creative Commons.

Figure 17. ***Porella navicularis***, a leafy liverwort used in nests of the Hammond's Flycatcher in the Pacific Northwest. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 18. ***Empidonax occidentalis***, Cordilleran Flycatcher. Members of this species often include mosses in their nests. Photo from Amado Demesa, through Creative Commons.

Figure 19. ***Sayornis nigricans***, Black Phoebe. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Eastern Phoebe (*Sayornis phoebe*)

I picked up my copy of "A Complete Field Guide to Nests in the United States" with eager anticipation. I quickly scanned the keys that depended on nesting location and materials and found several that mentioned mosses or peatlands. As I looked up each appropriate item in the key, I soon discovered only one bird was cited as a bryophyte user, the Eastern Phoebe – ***Sayornis phoebe*** (Figure 20) (Headstromn 1970). The Eastern Phoebe builds a cup-shaped nest (Figure 21) lined with mud and fibrous plant material. It uses mosses as a binding material with mud in the inner cup (Breil & Moyle 1976). It also uses mosses to line the cup. The outermost layer is also covered with moss (Headstromn 1970). Bent (1963) provided interesting bryological information. In a single nest, ***Mnium stellare*** (Figure 22), ***Funaria*** sp. (Figure 23), ***Polytrichum*** sp. (Figure 24), ***Hypnum*** "***cristatum***," and ***Climacium dendroides*** (Figure 25) were used as construction materials.

Figure 20. ***Sayornis phoebe***, Eastern Phoebe, a bird that can be identified by the mosses in its nest. Photo by John Benson, through Creative Commons.

Figure 21. ***Sayornis phoebe***, Eastern Phoebe, nest. Photo by Bernard Goffinet, through Creative Commons.

Figure 22. ***Mnium stellare***, a moss used in the Eastern Phoebe (***Sayornis phoebe***) nests. Photo by Hermann Schachner, through Creative Commons.

Figure 23. ***Funaria hygrometrica*** with immature capsules, a species used in nests of the Eastern Phoebe. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Polytrichum commune***, member of a genus used in construction of nests of the Eastern Phoebe. Photo by Hermann Schachner, through Creative Commons.

Figure 25. ***Climacium dendroides***, a moss used in nests of the Eastern Phoebe. Photo by Stan Phillips, through public domain.

Figure 26. ***Sayornis saya***, Say's Phoebe. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 27. ***Sayornis saya***, Say's Phoebe, nest with young. Photo by Tom Grey, with permission.

Figure 28. ***Pitangus sulphuratus***, Great Kiskadee. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Eastern Kingbird (*Tyrannus tyrannus*)

The Eastern Kingbird (***Tyrannus tyrannus***; Figure 29) of the Great Plains typically lives in forests where the canopy level is uneven, providing high points for observation and foraging (Johnsgard 2009). The female picks the nest site and builds the nest (Figure 30). She places it on outer branches of shrubs or small trees and often incorporates mosses in the construction.

Figure 29. ***Tyrannus tyrannus***, Eastern Kingbird. Members of this species often include mosses in their nests. Photo by MDF, through Creative Commons.

Figure 30. ***Tyrannus tyrannus***, Eastern Kingbird, nest with eggs. Photo by Anc516, through Creative Commons.

Figure 31. ***Tyrannus melancholicus***, Tropical Kingbird. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Figure 32. ***Tyrannus couchii***, Couch's Kingbird. Members of this species often include mosses in their nests. Photo by Ruben, through Creative Commons.

Figure 33. ***Tyrannus forficatus***, Scissor-tailed Flycatcher. Members of this species often include mosses in their nests.. Photo by Tom Grey, with permission.

Yellow-bellied Chat-tyrant (*Ochthoeca diadema*)

Miller and Greeney (2008) described the nest of the Yellow-bellied Chat-tyrant (***Ochthoeca diadema***; Figure 34). They found a partially domed cup built into a vertical mat of mosses that hung from a horizontal vine. The cup was thick and composed of bryophytes with a sparse lining of feathers. The dome covered only about one-third of the cup. Closer examination revealed that the nest was actually build into the vertical sheet of mosses.

Figure 34. ***Ochthoeca diadema***, Yellow-bellied Chat Tyrant. Members of this species sometimes build their nests into vertical hanging mats of mosses. Photo by Andres Cuervo, through Creative Commons.

Crowned Chat-tyrant (*Ochthoeca frontalis*)

Miller and Greeney (2008) found the Crowned Chat-tyrant (***Ochthoeca frontalis***) where it built its nest into a clump of mosses that was hanging 50 cm below a horizontal tree trunk (Miller & Greeney 2008). This provided good concealment by vegetation on the upper side. The nest was a partial dome made of mosses built into growing mosses and ferns.

Other species, such as Rufous-breasted Chat (***Ochthoeca rufipectoralis***; Figure 35) and Slaty-backed Chat-tyrant (***O. cinnamomeiventris***; Figure 36) also place their mossy cups on ledges (Hilty & Brown 1986; Greeney 2007).

Figure 35. ***Ochthoeca rufipectoralis***, Rufous-breasted Chat Tyrant. Members of this species often include mosses in their nests. Photo by Dick Cook, through Creative Commons.

Figure 36. ***Ochthoeca cinnamomeiventris***. Members of this species place mossy cups on ledges. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 37. ***Pachyramphus aglaiae***, Rose-throated Becard. Members of this species often include mosses in their nests. Photo by Dominic Sherony, through Creative Commons.

Laniidae – Shrikes

Wolf (2009) found two species of **Laniidae** that use bryophytes in their nests in North America:

Lanius ludovicianus (Loggerhead Shrike; Figure 38)
Lanius excubitor (Northern Shrike; Figure 39)

Figure 38. ***Lanius ludovicianus***, Loggerhead Shrike. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 39. ***Lanius excubitor***, Northern Shrike. Members of this species often include mosses in their nests. Photo by Smudge 9000, with permission.

Vireonidae – Typical Vireos

Wolf (2009) found three species of **Corvidae** that use bryophytes in their nests in North America:

Vireo griseus (White-eyed Vireo; Figure 40)
Vireo cassinii (Cassin's Vireo; Figure 41-Figure 42)
Vireo huttoni (Hutton's Vireo; Figure 43)

Figure 40. ***Vireo griseus***, White-eyed Vireo. Members of this species often include bryophytes in their nests. Photo by Andy Reago and Chrissy McClarren, through Creative Commons.

Figure 41. ***Vireo cassinii***, Cassin's Vireo. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 42. ***Vireo cassinii***, Cassin's Vireo, nest with female. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 43. ***Vireo huttoni***, Hutton's Vireo. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Rhipiduridae – Fantails

The Grey Fantail (***Rhipidura albiscapa***) in Tasmania builds a tidy nest of grass, moss sporophytes, bark, other plant fibers, ad spider webs (Lloyd 2013). The webs are used to attach the nest to a branch. The moss sporophytes are used to line the cup of the nest. These nests are built by the males and females in the understorey shrubs and small trees and both birds contribute to feeding.

Figure 44. ***Rhipidura albiscapa*** (Grey Fantail), a species that lines its nest with moss sporophytes. Photo by Patrick Kavanagh, through Creative Commons.

Figure 45. ***Rhipidura albiscapa*** (Grey Fantail) nest and nestlings. Photo by Benjamint444, through Creative Commons.

Monarchidae – Monarch Flycatchers

The Rarotonga Flycatcher (***Pomarea dimidiata***; Figure 46), an endangered species in the Cook Islands of Polynesia, makes a nest entirely from mosses (Figure 46-Figure 47), mostly **Meteoriaceae** (Figure 48) (John Game, Bryonet 22 June 2016).

Figure 46. ***Pomarea dimidiata***, Rarotonga Flycatcher, at mossy nest. Photo by G. McCormack © CINHP <www.cookislands.bishopmuseum.org>, with online permission.

Figure 47. ***Pomarea dimidiata***, Rarotonga Flycatcher, on nest of mosses. Photo by G. McCormack © CINHP <www.cookislands.bishopmuseum.org>, with online permission.

Figure 48. ***Weymouthia mollis***, member of **Meteoraceae** that is common in bird nests. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Myiagra cyanoleuca (Migratory Satin Flycatcher; Figure 49) builds a nest on a dead horizontal branch 5-25 m

above ground (Lloyd 2013). It uses bark strips and moss tightly bound with spider webs, making it neat and well disguised.

Figure 49. ***Myiagra cyanoleuca*** (Satin Flycatcher) male, a species that includes mosses in its nests. Aviceda at English Wikipedia, though Creative Commons.

Corvidae – Jays, Magpies, & Crows

Wolf (2009) found nine species of **Corvidae** that use bryophytes in their nests in North America:

Perisoreus canadensis (Gray Jay; Figure 50)
Cyanocitta stelleri (Steller's Jay; Figure 51)
Cyanocitta cristata (Blue Jay; Figure 52)
Cyanocorax yncas (Green Jay; Figure 53)
Aphelocoma californica (California Scrub-jay; Figure 54)
Gymnorhinus cyanocephalus (Pinyon Jay; Figure 55)
Nucifraga columbiana (Clark's Nutcracker; Figure 56)
Corvus brachyrhynchos (American Crow; Figure 57)
Corvus caurinus (Northwestern Crow; Figure 58)
Corvus corax (Common Raven; Figure 59)

Figure 50. ***Perisoreus canadensis***, Gray Jay. Members of this species often include mosses in their nests. Photo by Walter Siegmund, through Creative Commons.

Figure 51. ***Cyanocitta stelleri***, Steller's Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 52. ***Cyanocitta cristata***, Blue Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 53. ***Cyanocorax yncas***, Green Jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 54. ***Aphelocoma californica***, California Scrub-jay. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 55. ***Gymnorhinus cyanocephalus***, Pinyon Jay. Members of this species often include mosses in their nests. Photo by James St. John, through Creative Commons.

Figure 56. ***Nucifraga columbiana***, Clark's Nutcracker. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 57. ***Corvus brachyrhynchos***, American Crow. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 58. ***Corvus caurinus***, Northwestern Crow. Members of this species often include mosses in their nests. Photo by T Greyfox, through Creative Commons.

Common Raven (*Corvus corax*)

The Raven (***Corvus corax***; Figure 59) uses mosses to line its nest (Giannetta 2000).

Figure 59. ***Corvus corax***, Raven. Members of this species often include mosses in their nests. Photo by Dick Daniels, through Creative Commons.

Hirundinidae – Swallows

Wolf (2009) found only two species of **Hirundinidae** that use bryophytes in their nests in North America:

Tachycineta bicolor (Tree Swallow; Figure 60-Figure 61)
Stelgidopteryx serripennis (Northern Rough-winged Swallow; Figure 62)

Tree Swallow (*Tachycineta bicolor*)

Tree Swallows (***Tachycineta bicolor***; Figure 60) are known to construct a basket nest (Figure 61) of sticks with an "upholstery" of moss, grass, and animal fur (Heinrich 2000). Heinrich assumed these to provide insulation and to cushion the eggs.

Figure 60. ***Tachycineta bicolor***, Tree Swallow, male. Members of this species use bryophytes in their treehole nests. Photo by Tom Grey, with permission.

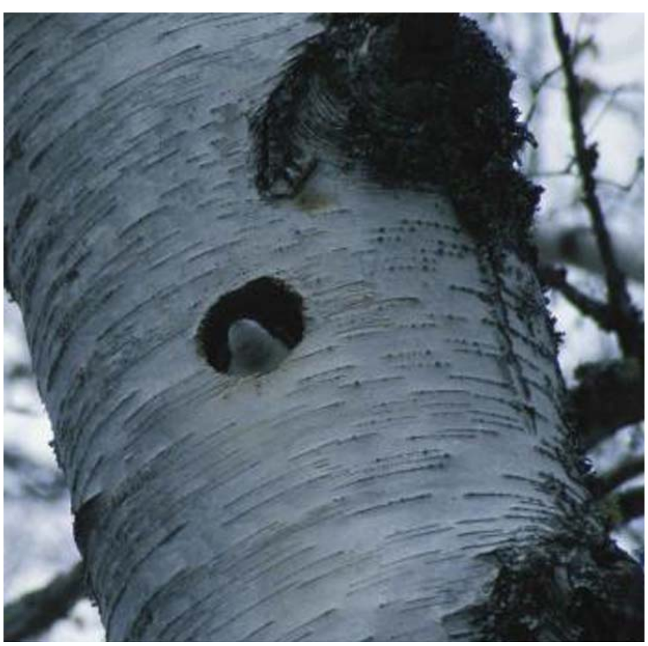

Figure 61. ***Tachycineta bicolor***, tree swallow, in a nest where bryophytes were used. Photo through public domain.

Figure 62. ***Stelgidopteryx serripennis***, Northern Rough-winged Swallow. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Paridae – True Tits

Wesołowski (unpublished data) found that the tits typically gathered moss for their nests in the immediate vicinity of the nest cavity, but they also would travel up to 80 m to gather nesting materials. Wolf (2009) found eight species of **Paridae** that use bryophytes in their nests in North America:

Poecile atricapillus (Black-capped Chickadee; Figure 74)
Poecile gambeli (Mountain Chickadee; Figure 89)
Poecile rufescens (Chestnut-backed Chickadee; Figure 90)
Poecile hudsonicus (Boreal Chickadee; Figure 91)
Poecile cinctus (Gray-headed Chickadee; Figure 92)
Baeolophus inornatus (Oak Titmouse; Figure 93)
Baeolophus ridgwayi (Juniper Titmouse; Figure 94)
Baeolophus bicolor (Tufted Titmouse; Figure 95)

Wesołowski and Wierzcholska (2018) compared the nesting materials used by three species of tit (Figure 63) and demonstrated that they were selective. Furthermore, the selections differed among the species. They avoided the abundant ***Brachythecium rutabulum*** (Figure 64), and ***Plagiothecium nemorale*** (Figure 65) and almost never used ***Anomodon longifolius*** (Figure 66) or ***Brachythecium oedipodium*** (Figure 67). Of the 54 available species, 21 were never used. Most plots associated with the nests had an average of 10.2-11.6 moss species/plot. The liverwort ***Metzgeria furcata*** (Figure 68) was used exclusively by Marsh Tits, and in greater proportion than in the environment. ***Brachythecium salebrosum*** was used only by Blue Tits, who also used large quantities of two forms of ***Hypnum cupressiforme*** (Figure 103). Great Tits under-used ***Hypnum cupressiforme*** forms but used ***Anomodon viticulosus*** (Figure 69), and possibly also ***Pleurozium schreberi*** (Figure 70) in greater proportion than their

availability. Wesołowski and Wierzcholska found no difference in water uptake between used and unused mosses. The Great Tits used mosses (***Anomodon viticulosus***, ***Isothecium alopecuroides*** (Figure 71), ***Pleurozium schreberi***) with stems twice as thick as those used by the Marsh Tits [***Hypnum cupressiforme*** mod. ***filiforme*** (Figure 72), ***Neckera complanata*** (Figure 73)].

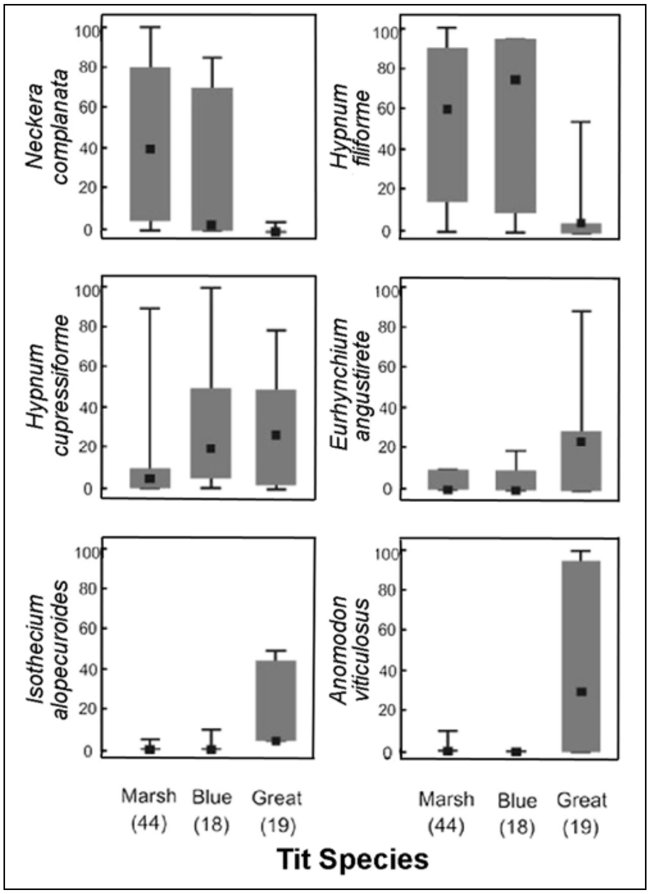

Figure 63. Moss choice in nests of three species of tits in Poland. The percent represents to the percent of volume of mosses in the moss layer of nests that had mosses. Small squares represent the medians, boxes indicate 25-75% quartiles, and whiskers show the ranges. Numbers in parentheses are sample sizes. Modified from Wesołowski & Wierzcholska 2018.

Figure 64. ***Brachythecium rutabulum***, an abundant moss avoided by tits. Photo by Janice Glime.

Figure 65. ***Plagiothecium nemorale***, an abundant moss that is avoided by tits as a nesting material. Photo by Michael Luth, with permission.

Figure 66. ***Anomodon longifolius***, an abundant moss that is rarely used by tits for their nests. Photo by Hermann Schachner, through Creative Commons.

Figure 67. ***Brachythecium oedipodium***, an abundant moss that is rarely used by tits for their nests. Photo by Michael Luth, with permission.

Figure 68. ***Metzgeria furcata***, a liverwort that often occurs in tit nests, but in small quantity. Photo by Michael Luth, with permission.

Figure 69. ***Anomodon viticulosus***, a preferred moss for nests by Great Tits. Photo by Janice Glime.

Figure 70. ***Pleurozium schreberi***, a preferred moss for nests of Great Tits. Photo by Janice Glime.

Figure 71. ***Isothecium alopecuroides*** with capsules, mosses with thick stems that preferred by Great Tits for nest materials. Photo by David T. Holyoak, with permission.

Figure 72. ***Hypnum cupressiforme*** mod. ***filiforme***, a moss with thin stems and that is used for nest materials by Marsh Tits. Photo by Jan-Peter Frahm, with permission.

Figure 73. ***Neckera complanata***, a moss with thin stems and that is used for nest materials by Marsh Tits. Photo by Michael Lüth, with permission.

But why did these birds travel as much as 80 m to gather some species when unused ones were much closer? When Wesołowski and Wierzcholska (2018) used human

plucking of the mosses used in nests and compared them to plucking of the unused species, they found that the used species yielded larger (heavier) bundles of moss and contained longer shoots than of those mosses that were ignored by the birds. This suggests that there is an energy benefit when using the selected species.

Black-capped Chickadee (*Poecile atricapillus*)

Allen (2017) observed a Black-capped Chickadee (***Poecile atricapillus***; Figure 74) busily gathering dry moss for its nest, then flying to the nestbox. The stream had lots of moss, but the bird ignored these, preferring the dry patch next to the stream. The Robin, on the other hand, preferred the wet moss for its open, mud-lined nest.

Figure 74. ***Poecile atricapillus***, Black-capped Chickadee. Members of this species gather dry mosses near a stream for their nests. Photo by Tattooed Dreamer, through Creative Commons.

Carolina Chickadee (*Poecile carolinensis*)

Erichsen (1919) describes the appearance of "down" on the cinnamon and royal ferns as a signal that the Carolina Chickadee (***Poecile carolinensis***; Figure 75) will begin its nest building (Figure 76). The Carolina Chickadee often begins this nest (Figure 77) by placing a thick mat of green moss (often ***Hypnum***; Figure 78) from the tree trunks into the nesting cavity (Figure 77). This always occurs first, followed by the soft down of the ferns.

Figure 75. ***Poecile carolinensis***, Carolina Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 76. ***Poecile carolinensis***, Carolina Chickadee, with nesting materials. Photo by Tom Grey, with permission.

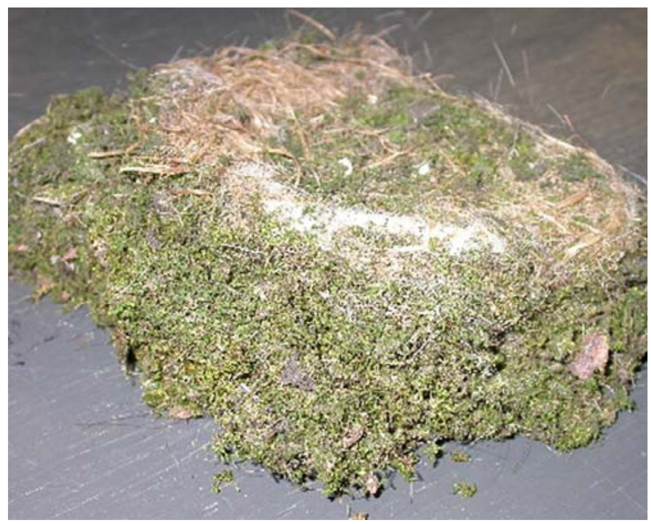

Figure 77. ***Poecile carolinensis***, Carolina Chickadee, nest. Photo courtesy of Diane Lucas.

Figure 78. ***Hypnum imponens***, a common species in a genus used for nests of the Carolina Chickadee. Photo by Janice Glime.

Andreas (2010) observed nests of two Carolina Chickadees (***Poecile carolinensis***; Figure 75). These included ten mosses and two liverworts. The dominant species were the pleurocarpous moss ***Platygyrium repens*** (Figure 79) and the leafy liverwort ***Frullania eboracensis*** (Figure 80) plus a few others, which comprised 55% of the nesting material by volume. In another year, the bryophytes comprised 70.4% of the nest material. The selection of bryophytes was not in proportion to their abundance and all species used were epiphytic on bark. Andreas suggested that they may select ***Frullania eboracensis*** for its chemical properties, possibly protecting them from mites (Figure 113). Only **corticolous** (growing on tree bark) bryophytes were used, with the exception of a single piece of ***Bryoandersonia illecebra*** (Figure 81) in one nest. But even clumps of **acrocarpous** (mostly upright with archegonia and capsules forming at tip of stem) mosses were removed from the tree trunks as tiny tufts for nest usage, including ***Orthotrichum ohioense*** and ***Dicranum montanum*** (Figure 82). Other corticolous bryophytes, including ***Anomodon attenuatus*** (Figure 83), ***Brachythecium laetum*** (Figure 84), ***Clasmatodon parvulus*** (Figure 85), ***Hypnum pallescens*** (Figure 86), and ***Ulota crispa*** (Figure 87), were ignored.

Figure 79. ***Platygyrium repens*** with bulbils, a moss used in nests of Carolina Chickadees. Photo by Hermann Schachner, through Creative Commons.

Figure 80. ***Frullania eboracensis***, a leafy liverwort used in nests of Carolina Chickadees. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 81. ***Bryoandersonia illecebra***, the only non-epiphytic moss used in a Carolina Chickadee nest. Photo by Bob Klips, with permission.

Figure 82. ***Dicranum montanum***, an acrocarpous moss used in the nest of a Carolina Chickadee. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Anomodon attenuatus*** with capsules, an epiphytic moss that was ignored when the Carolina Chickadee built its nest. Photo by Bob Klips, with permission.

Figure 84. ***Brachythecium laetum***, an epiphytic moss that was ignored when the Carolina Chickadee built its nest. Photo by Bob Klips, with permission.

Figure 85. ***Clasmatodon parvulus***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by A. Newman, through Creative Commons.

Figure 86. ***Hypnum pallescens***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by Michael Lüth, with permission.

Figure 87. ***Ulota crispa***, an epiphytic moss that was ignored when a Carolina Chickadee built its nest. Photo by Michael Lüth, with permission.

In Cashiers, NC, a Carolina Chickadee (***Poecile carolinensis***; Figure 75) used ***Thuidium delicatulum*** (Figure 88) in its nest in an English Boxwood shrub (Annie Martin, Bryonet 1 June 2010).

Figure 88. ***Thuidium delicatulum***, a ground moss used in the nest of a Carolina Chickadee. Photo by Janice Glime.

Figure 89. ***Poecile gambeli***, Mountain Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 90. ***Poecile rufescens***, Chestnut-backed Chickadee. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 91. ***Poecile hudsonicus***, Boreal Chickadee. Members of this species often include mosses in their nests. Photo by David Mitchell, through Creative Commons.

Figure 92. ***Poecile cinctus***, Grey-headed Chickadee. Members of this species often include mosses in their nests. Photo by Jargal Lamjav, through Creative Commons.

Figure 93. ***Baeolophus inornatus***, Oak Titmouse, with its nest in the large hole at the bottom left. Members of this species include bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 94. ***Baeolophus ridgwayi***, Juniper Titmouse. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Figure 95. ***Baeolophus bicolor***, Tufted Titmouse. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Varied Tit (*Sittiparus varius*)

The Varied Tit (***Sittiparus varius***; Figure 96) lives in coniferous forests, mixed forests, and bamboo in eastern Japan, Korea, and some parts of northeastern China and extreme southeastern Russia (southern Kurile Islands). It is one of the birds that uses bryophytes for nesting material (Sakai 2007).

Figure 96. ***Sittiparus varius***, Varied Tit. Members of this species often include mosses in their nests. Photo by Alpsdake, through Creative Commons.

Figure 97. ***Parus major***, Great Tit,. Members of this species often include bryophytes in their nests. Photo by Paul Gulliver, through Creative Commons.

Figure 98. ***Parus major***, Great Tit, nest with bryophytes and eggs. Photo by Oh Wei, through Creative Commons.

Blue Tit (*Cyanistes caeruleus*), Great Tit (*Parus major*), and Japanese Tit (*Parus minor*)

The Great Tit (***Parus major***; Figure 97-Figure 98) and the Blue Tit (***Cyanistes caeruleus***; Figure 99-Figure 101) both use mosses to build their nests (Figure 98) (Hribek 1985). Likewise, Gustavo Tomás and Andrew Spink (pers. comm. 2010) have collected mosses from a large number of Blue Tit (***Cyanistes caeruleus***) and Coal Tit (***Periparus ater***; Figure 102) nests in the Netherlands. The most common species in the nest is the locally common ***Hypnum cupressiforme*** (Figure 103). But other locally common species are not common in the nests, suggesting a preference. It appears that different species may be used in different parts of the nest, but so far there is no quantitative analysis available to support this. Figure 108 demonstrates the use of a ***Hypnum*** species (with ***Thuidium***) in the nest of an unknown bird in Pennsylvania, USA.

Figure 99. ***Cyanistes caeruleus***, Eurasian Blue Tit,. Members of this species build their nests with mosses. Photo by Francis C. Franklin, through Creative Commons.

Figure 100. ***Cyanistes caeruleus***, Blue Tit, mossy nest and eggs. Photo by Notts Ex Miner, through Creative Commons.

Figure 101. ***Cyanistes caeruleus***, Blue Tit, nest with moss and nestlings. Photo by Notts Ex Miner, through Creative Commons.

Figure 102. ***Periparus ater***, Coal Tit. Members of this species often include mosses in their nests, preferring ***Hypnum cupressiforme***. Photo by Aviceda, through Creative Commons.

Figure 103. ***Hypnum cupressiforme***, a preferred moss in the nests of Blue Tits and Coal Tits. Photo by Michael Lüth, with permission.

Although the population may use a wide variety of mosses, a few species of bryophytes typically comprise the nest. For example, the Japanese Tit, ***Parus minor***, used 21 species of bryophytes in the nests, but among 91% of the 47 nests, more than 50% of the volume was comprised of only three bryophyte species (Hamao *et al*. 2016). In this case, the preference seems to relate to a potential food source. The Japanese Tits preferred pleurocarpous mosses. In thse nests, seven species of moths emerged from the nesting material and were more frequent in nests with successful fledgine than in failed nests.

Figure 104. ***Parus minor***, Japanese Tit, a species that seems to be selctive in choice of mosses for its nests. Photo by Hyun-tae Kim, through Creative Commons.

In the Czech Republic, Hříbek (1985) found that Blue Tits (Figure 99-Figure 101) used mostly softer species (***Hypnum cupressiforme*** (Figure 103), ***Leptodictyum riparium*** (Figure 105), whereas the Great Tits used mostly the large-stemmed mosses such as ***Calliergonella cuspidata*** (Figure 106) and ***Rhytidiadelphus squarrosus*** (Figure 107).

Figure 105. ***Leptodictyum riparium***, a favorite nesting material of Blue Tits in the Czech Republic, with capsule. Photo by Michael Lüth, with permission.

Figure 106. ***Calliergonella cuspidata***, one of the nesting materials of Great Tits in the Czech Republic. Photo by David T. Holyoak, with permission.

Figure 107. ***Rhytidiadelphus squarrosus***, one of the nesting materials of Great Tits in the Czech Republic. Photo by Michael Lüth, with permission.

Álvarez *et al.* (2013) asserted that the properties and structure of a nest affect breeding performance. This drives the selection of behavior that produces nests characteristic of the species, including the appropriate nesting materials. Where preferred materials are low, birds select alternative materials, often at the cost of reduced breeding success. The researchers set out to support this hypothesis with the Great Tit, a species that has a wide range of habitats, using populations in four different Mediterranean habitats. Interestingly, the clutch size decreased as moss mass increased in the four sites. However, hatching success increased as the moss mass increased in one site. And in all the habitats, the nestling condition was poorer in nests with a greater proportion of sticks and feathers.

Mainwaring *et al.* (2012) reported that the nests of Blue Tits (***Cyanistes caeruleus***) and Great Tits (***Parus major***; Figure 97-Figure 98) in Great Britain consist of a "pad of moss mixed with dry grass and other plant material placed at the base of the nest box" (Figure 109) (Cramp & Perrins 1993; Mainwaring *et al.* 2008; Mainwaring & Hartley 2008, 2009; Britt & Deeming 2011). The nest cup is lined with fine dry grass, hair, wool and feathers. In this case, it appears that the mosses may be used to regulate the temperature and insulate the eggs and young birds. When temperatures increase, the female reduces the amount of lining material.

Figure 108. ***Hypnum*** and ***Thuidium*** in unidentified nest. Photo courtesy of Jeri Peck.

Figure 109. ***Parus major***, Great Tit, with eggs in nest on mosses. Photo by Notts Ex Miner, through Creative Commons.

When Great Tits (***Parus major***; Figure 97) built a second nest in nest boxes after rearing their first brood, they still used mosses in the nest, but there was no lining or inner layer – or any eggs (Slagsvold 1984).

Rydgren *et al*. (2023) compared the mosses used in nests of ***Parus major*** to those available nearby. There was a clear preference for highly branched pleurocarpous species, especially ***Pleurozium schreberi*** (Figure 70), ***Rhytidiadelphus squarrosus*** (Figure 107), and ***Sanionia uncinata*** (Figure 110). They avoid common species that are only sparsely branched. They also used the same species in the same nest boxes in subsequent years. The nesting materials were collected close to the nest, predominantly within 5 m, supporting the hypothesis that collecting nest materials is costly (Figure 111). The researchers suggested that studies are needed to reveal cost of gathering nest materials, to determine the suitability (advantages?) of the materials chosen, and to see if the choices are inherited. It would be interesting to run choice experiments with materials having a variety of properties and to compare nesting materials of the same species in different locations.

Figure 110. ***Sanionia uncinata***, a preferred species for nests of the Great Tit (***Parus major***). Photo by Claire Halpin, with permission.

Figure 111. ***Parus minor*** making nest with branched moss. Photo by Alpsdake, through Creative Commons.

The Corsican Blue Tit (***Cyanistes caeruleus ogliastrae***; Figure 112) includes 1-5 aromatic herbs in its nest (Lambrechts & Dos Santos 2000). Herbs are included in a number of kinds of bird nests, and researchers have suggested that they may serve an anti-parasite function (Figure 113) (Wimberger 1984; Bucher 1988; Cowie & Hinsley 1988; Clark 1991; Banbura *et al.* 1995). Using an herb removal experiment when the young hatched, these researchers found that the parents brought fresh aromatic greens to the nest. They proposed the Potpourri hypothesis that included at least seven functional causes for materials used in the nests. When the Blue Tits breed in cavities, they use predominately mosses, but also include other materials, including fresh herbaceous leaves. They suggested that mosses may optimize the microclimate in the nest cavity. The aromatic herbs are likely to serve an anti-parasitic function.

Figure 112. ***Cyanistes caeruleus ogliastrae***, Corsican Blue Tit. Members of this species often include mosses in their nests. Photo by Valter Jacinto, through Creative Commons.

Figure 113. ***Cyanistes caeruleus***, Eurasian Blue Tit, with mite infestation causing balding. Photo by Michael Palmer, through Creative Commons.

Ground Tit (*Pseudopodoces humilis*)

Ground Tit, also known as Hume's Jay, (***Pseudopodoces humilis***; Figure 114) has been considered the smallest member of the Jay and Crow family (Lipske 2004). But more recently it appears that it should be classified in the **Paridae** with the Chickadees. These birds are common in forests and woody suburbs of Europe and North America, but it appears that their ancestors lived on the dry, treeless Tibetan plateau. They nest in cavities where they build nests of grasses and mosses. Like Jays, they rarely fly, but they do not run like the Jays; rather, they hop.

Figure 114. ***Pseudopodoces humilis***, Ground Tit. Members of this species build nests of grasses and mosses. Photo by David Blank, through Creative Commons.

Pipridae – Manakins, Piprites

Black-capped Piprites (*Piprites pileata*)

Only one example in this family has emerged. The Black-capped Piprites (***Piprites pileata***; Figure 115) builds a spherical nest made of mosses (Cocckle *et al*. 2008).

Figure 115. ***Piprites pileata***, Black-capped Piprites. Members of this species often build their nests of mosses. Photo by Bruno Lima, through Creative Commons.

Aegithalidae – Long-tailed Tits

Wolf (2009) found one species of **Aegithalidae** whose members use bryophytes in their nests (Figure 116) in North America: ***Psaltriparus minimus*** (Bushtit; Figure 117).

Figure 116. ***Psaltriparus minimus***, Bushtit, at mossy nest. Photo by Walter Siegmund, through Creative Commons.

Figure 117. ***Psaltriparus minimus***, Bushtit, pulling on nest materials. Photo by Mikul, through Creative Commons.

Long-Tailed Tit (*Aegithalos caudatus*)

The Long-tailed Tit (***Aegithalos caudatus***; Figure 118-Figure 119) has been separated from other tits and has different feeding and nesting (Figure 120) habits from them. These are not seed-eaters, eating mostly insects from bark crevices and buds. The families stay together, so that a flock will contain only related birds. Relatives that have lost their family members will join the flock. Nests may be tended by 1-8 adults. The female sits on the eggs and the male brings the food. Once the dozen or more babies hatch, helper adults gather food to feed them.

Figure 118. ***Aegithalos caudatus***, Long-tailed Tit, a species whose members build nests with mosses. Photo by drplokta, through Creative Commons.

Figure 119. ***Aegithalos caudatus***, Long-tailed Tit juvenile. Photo by Charles J. Sharp, through Creative Commons.

Figure 120. ***Aegithalos caudatus***, Long-tailed Tit, building her nest in a hedgerow. Photo by Gail Hampshire, through Creative Commons.

The nests are bag-shaped and woven from mosses, bound with spider webs (Burton 1996). The birds cover the outside of the nest with lichens, sometimes substituting plastic and newspaper in areas of human habitation. This nest is insulated on the inside with feathers. The tits may accumulate ~1130 km of travel to gather nest materials. Hansell (2002) reported a nest with 5000-6000 pieces of material, including short-leaved mosses and cocoons intertangled, creating a Velcro effect with a few hundred sprigs of mosses.

Sittidae – Nuthatches

Wolf (2009) found two species of **Sittidae** that use bryophytes in their nests in North America:

Sitta carolinensis (White-Breasted Nuthatch; Figure 121)
Sitta pygmaea (Pygmy Nuthatch; Figure 123)

Figure 121. ***Sitta carolinensis***, White-breasted Nuthatch. Members of this species often include bryophytes in their nests. Photo by Tom Grey, with permission.

Red-Breasted Nuthatch (*Sitta canadensis*)

The Red-breasted Nuthatch (***Sitta canadensis***; Figure 122) builds its nest in tree holes, generally about 2.5 cm in diameter (Heinrich 2009; Moss Musings 2017). Inside the hole it lines the nest with mosses, down, and fibers. In fact, its nest can be recognized from those of woodpeckers because they never line their nests.

Figure 122. ***Sitta canadensis***, Red-breasted Nuthatch, outside the mossy nest in the treehole. Photo by Cephas, through Creative Commons.

Figure 123. ***Sitta pygmaea***, Pygmy Nuthatch, at tree hole. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission

Certhiidae – Holarctic Treecreepers

Wolf (2009) found one species of **Certhidae** whose members use bryophytes in their nests in North America: ***Certhia americana*** (Brown Creeper; Figure 124-Figure 125).

Figure 124. ***Certhia americana***, Brown Creeper, with a beak full of dinner. Photo by Alan and Elaine Wilson, through Creative Commons.

Figure 125. ***Certhia americana***, Brown Creeper, a bird that uses mosses to construct its nests. Photo by Badjoby, through Creative Commons.

Troglodytidae – Wrens

Wolf (2009) found five species of **Troglodytidae** that use bryophytes in their nests in North America:

Salpinctes obsoletus (Rock Wren; Figure 126)
Catherpes mexicanus (Canyon Wren; Figure 127)
Thryothorus ludovicianus (Carolina Wren; Figure 128-Figure 129)
Thryomanes bewickii (Bewick's Wren; Figure 130)
Troglodytes pacificus (Pacific Winter Wren; Figure 133-Figure 135)

Figure 126. ***Salpinctes obsoletus***, Rock Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

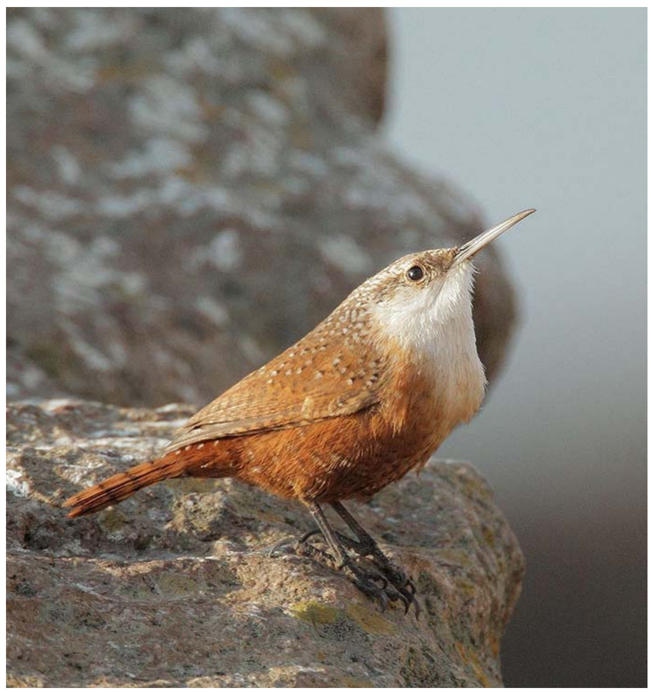

Figure 127. ***Catherpes mexicanus***, Canyon Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Carolina Wren (*Thryothorus ludovicianus*)

The tiny Carolina Wren (***Thryothorus ludovicianus***; Figure 128) is revered in places like Virginia because of its penchant for eating lots of insects (Harrison 2003). They nest mostly in nooks and crannies, so nest boxes are especially suitable for them. Their nests (Figure 129) often contain mosses, along with leaves, twigs, rootlets, weed stalks, and even cast-off snake skins. Both males and females are the nest builders, but it is she who lines the nest with feathers, hair, fine grass, and moss. These prolific breeders will typically lay a second set of eggs as soon as the young birds leave the nest and may even have a third set.

Figure 128. ***Thryothorus ludovicianus***, Carolina Wren. Members of this species often include mosses in their nests and nest linings. Photo by Ken Thomas, through public domain.

Figure 129. ***Thryothorus ludovicianus***, Carolina Wren, nest with a considerable proportion of mosses, and nestlings. Photo by Marvin, through Creative Commons.

Figure 130. ***Thryomanes bewickii***, Bewick's Wren. Members of this species often include mosses in their nests. Photo by Tom Grey, with permission.

Pacific Wren (*Troglodytes pacificus*) and Winter Wren (*T. hiemalis*)

The Winter Wren has been divided into two species, the Pacific Wren (***Troglodytes pacificus***; Figure 131) and the Winter Wren (***Troglodytes hiemalis***; Figure 132), the eastern species (Toews & Irwin 2008). Where their breeding ranges overlapped, the two species were distinguishable by their songs and lack of cross mating. This evidence was supported by DNA analysis.

Figure 131. ***Troglodytes pacificus***, Pacific Wren. Members of this species often include mosses in their nests. Photo by Tom Talbott, through Creative Commons.

The Pacific Wren (***Troglodytes pacificus***; Figure 131) breeds in the coniferous forests of the Pacific Northwest and constructs a nest almost entirely of mosses (Hejl *et al.* 2002). These wrens protect their nests with a dome and small side entrance (Heinrich 2009). The winter wren places green mosses and small evergreen twigs on the outside. Some birds place their nests in hanging mosses near the ground, but more commonly they place them on tip-up mounds formed by roots of fallen trees.

The Pacific Wren builds a round nest of grass, moss, lichens, or leaves that it stuffs into a hole in a wall, crack in a rock, corner of a building, or tree trunk, but can also put it in bushes or overhanging boughs (Wikipedia 2010).

Eastern Winter Wren (*Troglodytes hiemalis*)

Piers (1897) reported two Winter Wren (***Troglodytes hiemalis***; Figure 132) nests in Nova Scotia, Canada, built in moss that was constantly saturated by water trickling from the bank above. Piers suspected that the second nest was a later one built by the same pair as the first.

Figure 132. ***Troglodytes hiemalis***, Winter Wren. Members of this species often include mosses in their nests. Photo by Paul Stein, through Creative Commons.

Eurasian Wren (*Troglodytes troglodytes*)

Nests of the Eurasian Wren (***Troglodytes troglodytes***; Figure 133) can make its nest almost entirely of bryophytes (Figure 134). The Japanese variety (***Troglodytes troglodytes fumigatus***) likewise uses mosses (Figure 135).

Figure 133. ***Troglodytes troglodytes***, Eurasian Wren, a bryophyte nest builder. Photo by Dibyendu Ash, through Creative Commons.

Figure 134. ***Troglodytes troglodytes***, Eurasian Wren, feeding young in nest of mosses and other materials. Photo by Sonja Kübelbeck, through Creative Commons.

Figure 135. ***Troglodytes troglodytes fumigatus***, Japanese Winter Wren, shown here gathering mosses for its nest. Photo by Alpsdake, through Creative Commons.

Cinclidae – Dippers

Wolf (2009) found one species of **Cinclidae** whose members use bryophytes in their nests in North America: ***Cinclus mexicanus*** (American Dipper; Figure 136-Figure 137), also known as the Water Ouzel.

Figure 136. ***Cinclus mexicanus***, American Dipper, on mosses on the streambank. Photo by Stephen Shunk, through Creative Commons.

Figure 137. ***Cinclus mexicanus***, American Dipper, gathering moss for its nest. Photo by Frank D. Lospalluto, through Creative Commons.

The American Dipper (Figure 136-Figure 137) is the only aquatic songbird in North America (Rosentreter 2014). It is a year-round resident, maintaining its streamside territorial defense year-round. It is known for its diving ability, down to nearly 7 m below the surface, and lives along unpolluted streams with riffles, cascades, and waterfalls. It makes a ball-shaped nest with a side entrance, placed on a cliff face, in a crevice, or under a bridge abutment, positions that help it to avoid predators. The outer shell of this nest is moss with its inner chamber made of pine needles. It uses stream mosses that it dives to obtain, hence they are dripping wet. These are woven into the nest, still wet, and as they dry they tighten the weave and help to affix the nest to its vertical substrate.

I have seen the nest of an American Dipper (Figure 136-Figure 137) in Colorado with the busy expectant mother diving into the water to collect ***Platyhypnidium riparioides*** (Figure 138) for the construction. The nest (Figure 139), wedged under the cliff behind a waterfall, appeared to be made entirely of mosses. Dan Norris (Bryonet 22 November 1995) reports that this bird is indeed selective, using mosses with a different frequency from that found in their habitat.

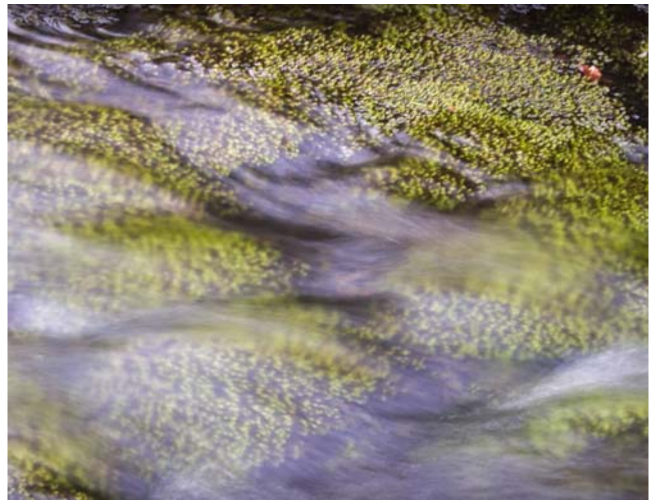

Figure 138. ***Platyhypnidium riparioides***, a common moss used in nests of the American Dipper (***Cinclus mexicanus***). Photo by Stan Phillips, through public domain.

Figure 139. ***Cinclus mexicanus***, American Dipper, nest of ***Hygrohypnum*** and ***Hygroamblystegium***. Photo by Janice Glime.

Terry McIntosh (Bryonet 2 June 2010) identified mosses in Dipper (***Cinclus mexicanus***; Figure 136-Figure 137) nests from northern Idaho. To his surprise, he found only one species, ***Scouleria marginata*** (Figure 140), a somewhat rare moss, despite the much greater abundance of ***S. aquatica*** (Figure 141). He attributed this selection to the stronger plants of ***S. marginata***. By contrast, Ellen Anderson (Bryonet 2 June 1010) found 30 moss species and 5 liverwort species (plus a few unknowns) in 7 dipper nests in the area around Juneau, Alaska, USA. Most of the nests had only traces of mosses, but nevertheless had quite a few species, numbering 1, 7, 10, 11, 13, 14, and 16 (plus 5 unknowns).

Figure 140. ***Scouleria marginata***, a common component of the American Dipper nests. Photo by Martin Hutten, with permission.

Figure 141. ***Scouleria aquatica***, a common moss that is ignored as nesting material for the American Dipper when ***S. marginata*** is present. Photo by Matt Goff, with permission.

Roger Rosentreter (pers. comm. 20 January 2014) observed numerous American Dipper (***Cinclus mexicanus***; Figure 136-Figure 137) nests on the Payette River, Idaho, USA, reaching up to 2 nests per kilometer. In this case, the nests were composed primarily of the aquatic moss ***Scouleria aquatica*** (Figure 141), an abundant moss in the river.

Brown Dipper (*Cinclus pallasii*)

The Brown Dipper, also known as the Pallas Dipper, (***Cinclus pallasii***; Figure 142), is an Asian dipper that uses mosses in its nests (Nishimura *et al.* 1980).

Figure 142. ***Cinclus pallasii pallasii***, Brown Dipper, a bird that uses aquatic bryophytes in its nests Photo by Alpsdake, through Creative Commons.

Summary

The Passeriformes is the largest order of birds and contains the majority of birds that use bryophytes in their nests. Nevertheless, they seem to be a small proportion of the total species in the order.

In this first part, the members using bryophytes include Tyrant Flycatchers, shrikes, Vireos, Jays and Crows, Swallows, Tits, Piprites, Nuthatches, and Wrens. Among these, the American Dipper is an aquatic bird that often dives for mosses to build its nest. Their selective choices may be energy savings by being able to gather larger bryophyte materials, providing nest-inhabiting food organisms, and in some cases possibly providing more constant moisture.

Acknowledgments

Thank you to Brian Dykstra for sending me the wonderful thesis on birds and epiphytes by Adrian Wolf, as well as other references and personal observations. David Dumond shared the references he got from Bryonet. Many photographers have provided permission or put their images in Creative Commons, for which I am deeply appreciative. Thank you to Tom Grey and Janet Marr for a critical reading of the manuscript. And thank you to

Bernard Goffinet for his continued support in sending me images and interesting publications.

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CHAPTER 16-7
BIRD NESTS – PASSERIFORMES, PART 2

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CHAPTER 16-7
BIRD NESTS – PASSERIFORMES, PART 2

Figure 1. ***Grallaricula peruviana*** is a rare bird, shown here with bryophytes in its nest. Photo by Harold Greeney, through Creative Commons

Grallariidae

The Peruvian Antpitta (***Grallaricula peruviana***) is a rare species that uses bryophytes in its nest, as seen in Figure 1.

Regulidae – Kinglets

Wolf (2009) found two species of **Regulidae** that use bryophytes in their nests in North America:

Regulus satrapa (Golden-Crowned Kinglet; Figure 2)
Regulus calendula (Ruby-Crowned Kinglet; Figure 4)

Figure 2. ***Regulus satrapa***, Golden-crowned Kinglet. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

The Golden-crowned Kinglet (***Regulus satrapa***; Figure 2) breeds in the coniferous forests (Figure 3) of the Pacific Northwest and constructs a nest almost entirely of mosses (Ingold & Galati 1997).

Figure 3. Conifer forest, Garibaldi National Park, BC, home to the Golden-crowned Kinglet, ***Regulus satrapa***. Photo by The Simkin, through public domain.

Figure 4. ***Regulus calendula***, Ruby-crowned Kinglet. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Sylviidae – Old-World Warblers & Gnatcatchers

Wolf (2009) found one species of **Sylviidae** that use bryophytes in their nests in North America: ***Phylloscopus borealis*** (Arctic Warbler; Figure 5).

Figure 5. ***Phylloscopus borealis***, Arctic Warbler. Members of this species use bryophytes in their nests. Photo by Osado, through Creative Commons.

Turdidae – Thrushes

Wolf (2009) found thirteen species of **Turdidae** that use bryophytes in their nests in North America:

Luscinia svecica (Bluethroat; Figure 6)
Oenanthe oenanthe (Northern Wheatear; Figure 7)
Sialia mexicana (Western Bluebird; Figure 8)
Myadestes townsendi (Townsend's Solitaire; Figure 9)
Catharus fuscescens (Veery; Figure 11)
Catharus minimus (Gray-Cheeked Thrush; Figure 12)
Catharus bicknelli (Bicknell's Thrush; Figure 13)
Catharus ustulatus (Swainson's Thrush; Figure 14)
Catharus guttatus (Hermit Thrush; Figure 15-Figure 16)
Turdus pilaris (Fieldfare; Figure 18-Figure 19)
Turdus iliacus (Redwing; Figure 20)
Turdus migratorius (American Robin; Figure 21-Figure 22)
Ixoreus naevius (Varied Thrush; Figure 38)

Figure 6. ***Luscinia svecica***, Bluethroat. Members of this species use bryophytes in their nests. Photo by Andreas Trepte, through Creative Commons.

Figure 7. ***Oenanthe oenanthe***, Northern Wheatear. Members of this species use bryophytes in their nests. Photo by Craig Nash, through Creative Commons.

Figure 8. ***Sialia mexicana***, Western Bluebirds. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 9. ***Myadestes townsendi***, Townsend's Solitaire. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 10. ***Myadestes palmeri***, Puaiohi, nest in a mossy cavity. Photo by Lucas Behnke, with permission.

Figure 11. ***Catharus fuscescens***, Veery. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 12. ***Catharus minimus***, Gray-cheeked Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 13. ***Catharus bicknelli***, Bicknell's Thrush, on mossy nest. Photo by Kent McFarland, through Creative Commons.

Figure 14. ***Catharus ustulatus***, Swainson's Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 15. ***Catharus guttatus***, Hermit Thrush. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Figure 16. ***Catharus guttatus***, Hermit Thrush nest and hatchlings. Photo by Per ver Donk, with permission.

Hermit Thrush (*Catharus guttatus*)

Once again, the female is the sole nest-builder in the Hermit Thrush (***Catharus guttatus***; Figure 15-Figure 16) (Cornell Lab of Ornithology). Her bulky handiwork includes mosses in addition to twigs, bark strips, ferns, and grasses. It is not lined with mosses, but rather with conifer needles, rootlets, and plant fibers.

Figure 17. Bird nest in Coast Range of the Pacific Northwest, USA, with mosses still growing. Photo by JeriLynn Peck.

Figure 18. ***Turdus pilaris***, Fieldfare. Members of this species use bryophytes in their nests. Photo by Allan Drewitt, through Creative Commons.

Figure 19. ***Turdus pilaris***, Fieldfare, nest, showing occasional mosses mixed with grasses in the nest. Photo by Andreas Trepte, through Creative Commons.

Figure 20. ***Turdus iliacus***, Redwing. Members of this species use bryophytes in their nests. Photo by Ómar Runólfsson, through Creative Commons.

American Robin (*Turdus migratorius*)

The American Robin (***Turdus migratorius***; Figure 21) uses mosses as a binding material with mud in the inner cup of the nest (Figure 22-Figure 23) (Breil & Moyle 1976). It also uses mosses to line the cup. It seems to have a preference for ***Thuidium delicatulum*** (Figure 24), ***Plagiomnium cuspidatum*** (Figure 25), ***Brachythecium acuminatum*** (Figure 26), ***B. salebrosum*** (Figure 27), and ***Amblystegium varium*** (Figure 28).

Figure 21. ***Turdus migratorius***, American Robin. Members of this species sometimes use mosses as a binder for the mud linings of their nests. Photo by Tom Grey, with permission.

Figure 22. ***Turdus migratorius***, American Robin, on nest. Photo by Jane and Phil, through Creative Commons.

Figure 23. ***Turdus migratorius***, American Robin, nest and young. Photo by Tom Grey, with permission.

Figure 24. ***Thuidium delicatulum***, a moss used as a mud binder to line the Robin's nest. Photo by Janice Glime.

Figure 25. ***Plagiomnium cuspidatum***, a moss used as a mud binder to line the Robin's nest. Photo by Hermann Schachner, through Creative Commons.

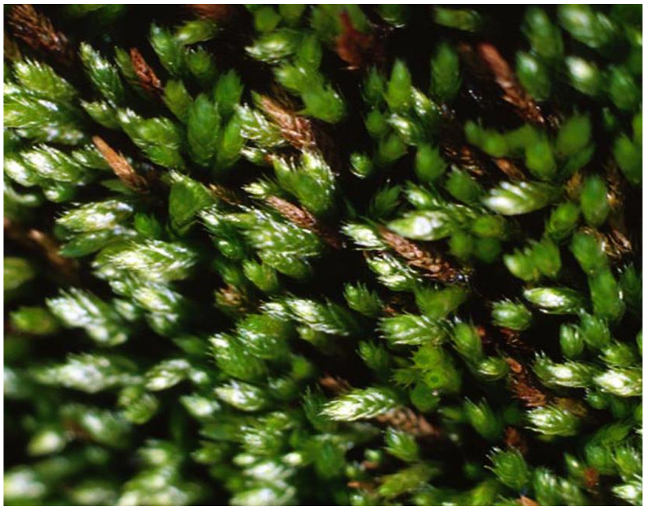

Figure 26. ***Brachythecium acuminatum***, a moss used as a mud binder to line the Robin's nest. Photo by Charles T. Bryson, through Creative Commons.

Figure 27. ***Brachythecium salebrosum*** with capsules, a moss used as a mud binder to line the Robin's nest. Photo by Michael Lüth, with permission.

Figure 28. ***Amblystegium varium***, a moss used as a mud binder to line the Robin's nest. Photo by J. C. Schou, through Creative Commons.

Other members of the genus, such as the Yellow-legged Thrush (***Turdus flavipes***; Figure 29-Figure 30), place bryophytes on the outside of the nest.

Figure 29. ***Turdus flavipes***, Yellow-legged Thrush. Members of this species use mosses on the outsides of their nests. Photo by David R. Santiago, through Creative Commons.

Figure 30. ***Turdus flavipes***, Yellow-legged Thrush, nest with eggs and bryophytes. Photo by David R. Santiago, through Creative Commons.

Chinese Thrush (*Turdus mupinensis*)

In a Chinese study (Zhao *et al*. 2005), nests of the Chinese Thrush (***Turdus mupinensis***; Figure 31) were collected from Xiaolongmen Nature Reserve of Beijing. Nests exhibited seven bryophyte species: ***Anomodon*** sp., ***A. minor*** (Figure 32), ***Entodon*** sp. (Figure 33), ***Lindbergia sinensis*** (see Figure 34), ***Brachythecium*** sp. (see Figure 27), ***Herpetineuron*** sp. (Figure 35), ***Plagiomnium*** sp. (see Figure 25), and ***Myuroclada maximowiczii*** (Figure 36). ***Anomodon minor*** was one of the major nest components.

Figure 31. ***Turdus mupinensis***, Chinese Thrush. Members of this species use mosses in their nests in China. Photo by Charles Lam, through Creative Commons.

Figure 32. ***Anomodon minor***, a species that is used in nests of the Chinese Thrush. Photo by Michael Lüth, with permission.

Figure 33. ***Entodon concinnus***, in a genus that is used in nests of the Chinese Thrush. Photo by Hermann Schachner, through Creative Commons.

Figure 34. ***Lindbergia koelzii*** with capsules, member of a genus used in nests of the Chinese Thrush, ***Turdus mupinensis***. Photo by Michael Lüth, with permission.

Figure 35. ***Herpetineuron toccoae***, member of a genus used in nests of the Chinese Thrush, ***Turdus mupinensis***. Photo by Li Zhang, with permission.

Figure 36. ***Myuroclada maximoviczii***, a species that is used in nests of the Chinese Thrush. Photo by Janice Glime

Blackbird (*Turdus merula*)

The Common Blackbird (***Turdus merula***; Figure 37) makes a bulky cup in its nest, using dry grasses, twigs, stalks, and yes, mosses (Snow 1958). These are plastered with mud or muddy leaves and lined with fine grass, thin dead stems, or rootlets. Mainwaring *et al.* (2014) found that as spring temperatures increased in the lower latitudes, the quantity of mosses used in the nests decreased, suggesting that mosses may be needed for insulation at cooler temperatures (Mainwaring *et al.* 2012).

Figure 37. ***Turdus merula***, Common Blackbird, nesting. Members of this species use bryophytes in their nests. Photo by J. J. Harrison, through Creative Commons.

Nest size of birds is limited on the upper end by becoming more conspicuous and requiring more energy to prepare (Møller 1990). On the small end, it loses insulating ability, stability, and protection to prevent nestlings from falling out of the nest. Møller manipulated nest size of the Blackbird (***Turdus merula***; Figure 37), a species that makes an open-cup woodland nest. When nests were exchanged for smaller or larger nests, there was no effect on nest egg predation by the exchange itself, but larger nests experienced more predation. But real nests that experienced predation were not significantly larger than successful nests. Møller suggested that nest size in nature is dependent on nest site.

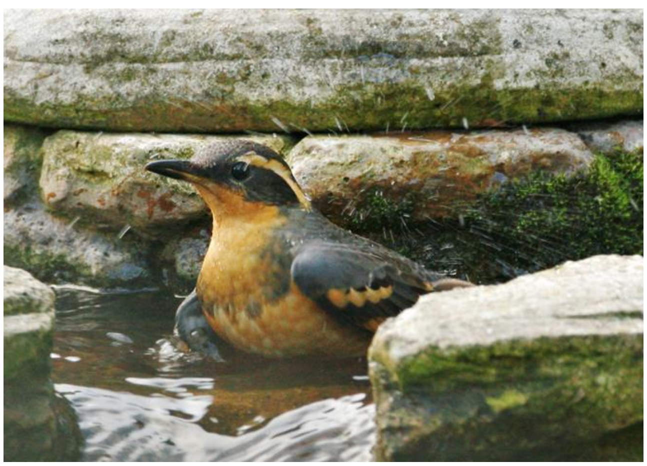

Figure 38. ***Ixoreus naevius***, Varied Thrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Muscicapidae – Old World Flycatchers

In the same Chinese study (Zhao *et al*. 2005), nests of three members of this family [Narcissus Flycatcher (***Ficedula narcissina***; Figure 39), Blue-and-white Flycatcher (***Cyanoptila cyanomelana***; Figure 40-Figure 41), Daurian Redstart (***Phoenicurus auroreus***; Figure 42)] were collected from Xiaolongmen Nature Reserve of Beijing. These nests, like those of the Chinese Thrush, exhibited the same seven bryophyte species, with the moss ***Anomodon minor*** (Figure 32) as the main component of nests of all three bird species.

Figure 39. ***Ficedula narcissina***, a Chinese species. Members of this species use bryophytes in their nests. Photo by Alpsdake, through Creative Commons.

Figure 40. ***Cyanoptila cyanomelana***, Blue-and-white Flycatcher male, a species that uses bryophytes to make nests. Photo by Alpsdake, through Creative Commons.

Figure 41. ***Cyanoptila cyanomelana***, Blue-and-white Flycatcher male. Members of this species make their nests with bryophytes. Photo by Alpsdake, through Creative Commons.

Figure 42. ***Phoenicurus auroreus***, Daurian Redstart male. Members of this species use bryophytes in their nests. Photo by Alpsdake, through Creative Commons.

Petroicidae – Australian Robins

Australian Pink Robin (*Petroica rodinogaster*)

The **Australian Pink Robin** (***Petroica rodinogaster***; Figure 43) includes both lichens and mosses in its nest (Figure 44) (Newman & Bratt 1976).

Figure 43. ***Petroica rodinogaster***, Australian Pink Robin. Members of this species build their nests of mosses, especially ***Thuidiopsis sparsa***. Photo by J. J. Harrison, through Creative Commons.

Pharo and Meagher (2011) reported finding a Pink Robin's nest that was made almost entirely from mosses. It was located in a mountain ash forest in Victoria, Australia, in an area that had been lightly burned two years earlier. The nest was "extraordinarily tiny on a branch of *Olearia agrophylla*." The nest was woven exclusively from ***Thuidiopsis sparsa*** (Figure 45) except for a few strands of grass. It is interesting that the moss was not even growing at the site. Therefore, the birds deliberately hunted that moss. The nest has a loose weave, but was strong, with intertwined moss branches. The nest was attached to a branch by numerous strands that were wrapped around the main branch and a smaller branch.

Figure 44. The tiny Australian Pink Robin's nest woven from ***Thuidiopsis sparsa*** (Figure 45), with Emma´s index finger for 'scale.' Photo courtesy of Emma Pharo and David Meagher.

Figure 45. ***Thuidiopsis sparsa***, a moss used to make the nest of the Australian Pink Robin (***Petroica rodinogaster***). Photo through Creative Commons.

Sturnidae – Starlings, *etc.*

Wolf (2009) found one species of **Sturnidae** whose members use bryophytes in their nests in North America: European Starling (***Sturnus vulgaris***; Figure 46-Figure 47).

Figure 46. ***Sturnus vulgaris***, European Starling, the only member of this family that uses mosses in its nest in North America. Photo by Ingrid Taylar, through Creative Commons.

Figure 47. ***Sturnus vulgaris***, European Starling, at nest. Photo by Gynti 46, through Creative Commons.

The European Starling "prefers" to use the wild carrot *Daucus carota* (Figure 48) or the fleabane *Erigeron philadelphicus* (Figure 49) in its nest, both of which have known abilities to suppress parasitic mites in nests (Clark & Mason 1985). We can only wonder if the bryophytes might serve a protective role against mites and other parasites in forested sites.

Figure 48. *Daucus carota* leaves, a species included in nests of the European Starling, presumably to reduce parasite infections. Photo by BioImages, through Creative Commons.

Figure 49. *Erigeron philadelphicus*, a species included in nests of the European Starling, presumably to reduce parasite infections. Photo by Fritzflohr Reynolds, through Creative Commons.

Motacillidae – Wagtails & Pipits

Wolf (2009) found one species of **Motacillidae** whose members use bryophytes in their nests in North America:

Motacilla alba (White Wagtail; Figure 50-Figure 51)
Anthus cervinus (Red-throated Pipit; Figure 54)
Anthus rubescens (American Pipit; Figure 55)

White Wagtail (*Motacilla alba*)

Des Callaghan (Bryonet 23 June 2016) reported that while in the wonderful north of Finland one summer, a fine place for **Splachnaceae**, he noticed an intriguing association between ***Splachnum vasculosum*** (Figure 52-Figure 53) and the insectivorous passerine bird ***Motacilla alba*** (Figure 50). Could the Wagtails be attracted by the odor? Are the mosses a food source? Or do the ***S. vasculosum*** and ***Motacilla alba*** simply like the same habitat? Callaghan recorded this interesting habitat <https://youtu.be/DdlJ7njn3Vg>. Mosses are included in nests (Figure 51) of this wagtail species (Bouglouan 2016).

Figure 50. ***Motacilla alba alba***, White Wagtail. Members of this species use bryophytes in their nests. Photo by Luis Garcia, through Creative Commons.

Figure 51. ***Motacilla alba***, White Wagtail, nest with eggs, a nest that often includes bryophytes. Photo by Walcoford, through Creative Commons.

Figure 52. ***Splachnum vasculosum*** colony, a preferred perch for White Wagtail (***Motacilla alba***). Photo by Des Callaghan, with permission.

Figure 53. ***Splachnum vasculosum*** with capsules and males. Photo by Dick Haaksma, with permission.

Figure 54. ***Anthus cervinus***, Red-throated Pipit. Members of this species use bryophytes in their nests. Photo by Tom Grey with permission.

Figure 55. ***Anthus rubescens***, American Pipit, with insect. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Small Kauai Thrush (*Myadestes palmeri*)

The Small Kauai Thrush or Puaiohi (***Myadestes palmeri***; Figure 56), a small Hawaiian endemic, builds a cavity nest (Figure 57) along a stream bank comprised mostly of bryophytes and tiny ferns, with a weave of fine grass (Kepler & Kepler 1983). The bryophytes trail out of the cavity mouth from the base of the nest, providing an opportunity for these bryophytes to attach and grow on the stream bank. Included bryophytes were the mosses ***Dicranum speirophyllum*** (Figure 58) and ***Campylopus*** sp. (Figure 59) and the liverworts ***Bazzania*** sp. (Figure 60) and ***Lepidozia*** sp. (Figure 61).

Figure 56. ***Myadestes palmeri***, Small Kauai Thrush. Members of this species use bryophytes in their nests. Photo by Eike Wulfmeyer, through Creative Commons.

Figure 57. ***Myadestes palmeri***, Puaiohi, nest with mosses in a cavity. Photo by Lucas Behnke, with permission.

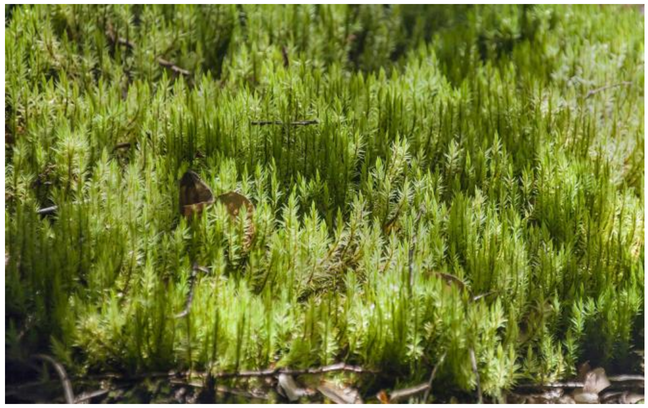

Figure 58. ***Dicranum speirophyllum***, a moss used in the Puaiohi (***Myadestes palmeri***) nest. Photo by John Game, through Creative Commons.

Figure 59. ***Campylopus umbellatus***, a moss representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Michael Lüth, with permission.

Figure 60. ***Bazzania*** sp., a leafy liverwort representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Ondřej Zicha, through Creative Commons.

Figure 61. ***Lepidozia*** sp., a leafy liverwort representing a genus used in the Puaiohi (***Myadestes palmeri***) nest. Photo by Ken-ichi Uedo, through Creative Commons.

Bombycillidae – Waxwings

Wolf (2009) found two species of **Bombycillidae** that use bryophytes in their nests in North America:

Bombycilla garrulus (Bohemian Waxwing; Figure 62)
Bombycilla cedrorum (Cedar Waxwing; Figure 63-Figure 64)

Figure 62. ***Bombycilla garrulus***, Bohemian Wax Wing. Members of this species use bryophytes in their nests. Photo by Randen Pederson, through Creative Commons.

Cedar Waxwing (*Bombycilla cedrorum*)

The Cedar Waxwing (***Bombycilla cedrorum***; Figure 63) nests in edge habitat, using small evergreens and deciduous trees to hold its nests (Figure 64) (Heinrich 2009). The nest is somewhat similar to that of a Robin in size and rough appearance, but it has no mud lining. The outside typically is decorated with lichens and mosses, probably providing camouflage.

Figure 63. ***Bombycilla cedrorum***, Cedar Waxwing. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 64. ***Bombycilla cedrorum***, Cedar Waxwing, nest with moss & eggs. Photo by Rich Mooney, through Creative Commons.

Peucedramidae – Olive Warbler

Wolf (2009) found one species of **Peucedramidae** that uses bryophytes in their nests in North America: ***Peucedramus taeniatus*** (Olive Warbler; Figure 65).

Figure 65. ***Peucedramus taeniatus***, Olive Warbler. Members of this species use bryophytes in their nests. Photo by Ron Knight, through Creative Commons.

Parulidae – Wood Warblers, *etc.*

Wolf (2009) found 27 species of **Parulidae** that use bryophytes in their nests in North America:

Oreothlypis ruficapilla (Nashville Warbler; Figure 67)
Oreothlypis celata (Orange-crowned Warbler; Figure 66, Figure 68)
Oreothlypis virginiae (Virginia's Warbler; Figure 69)
Dendroica coronata (Yellow-rumped Warbler; Figure 70)
Setophaga pitiayumi (Tropical Parula; Figure 71)
Setophaga magnolia (Magnolia Warbler; Figure 72)
Setophaga tigrina (Cape May Warbler; Figure 73)
Setophaga caerulescens (Black-throated Blue Warbler; Figure 74-Figure 75)
Setophaga nigrescens (Black-throated Gray Warbler; Figure 76)
Setophaga virens (Black-throated Green Warbler; Figure 77)
Setophaga townsendi (Townsend's Warbler; Figure 78)
Setophaga occidentalis (Hermit Warbler; Figure 79)
Setophaga kirtlandii (Kirtland's Warbler; Figure 80)
Setophaga striata (Blackpoll Warbler; Figure 81)
Setophaga cerulea (Cerulean Warbler; Figure 82)
Setophaga ruticilla (American Redstart; Figure 83)
Setophaga citrina (Hooded Warbler; Figure 84-Figure 85)
Protonotaria citrea (Prothonotary Warbler; Figure 86)
Helmitheros vermivorum (Worm-eating Warbler; Figure 88)
Limnothlypis swainsonii (Swainson's Warbler; Figure 90)
Seiurus aurocapilla (Ovenbird; Figure 91-Figure 92)
Parkesia noveboracensis (Northern Waterthrush; Figure 97)
Parkesia motacilla (Louisiana Waterthrush; Figure 98)
Oporornis agilis (Connecticut Warbler; Figure 99)
Geothlypis trichas (Common Yellowthroat; Figure 100)
Cardellina pusilla (Wilson's Warbler; Figure 101)
Cardellina canadensis (Canada Warbler; Figure 102)

Figure 66. ***Oreothlypis celata***, Orange-crowned Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 67. ***Oreothlypis ruficapilla***, Nashville Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 68. ***Oreothlypis celata***, Orange-crowned Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 69. ***Oreothlypis virginiae***, Virginia's Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 70. ***Dendroica coronata***, Yellow-rumped Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 71. ***Setophaga pitiayumi***, Tropical Parula. Members of this species use bryophytes in their nests. Photo by Dario Sanchez, through Creative Commons.

Figure 72. ***Setophaga magnolia***, Magnolia Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 73. ***Setophaga tigrina***, Cape May Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 74. ***Setophaga caerulescens***, Black-throated Blue Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 75. ***Setophaga caerulescens***, Black-Throated Blue Warbler, feeding young in nest. Members of this species use bryophytes in their nests. Photo by USFWS, through public domain.

Figure 76. ***Setophaga nigrescens***, Black-throated Gray Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 77. ***Setophaga virens***, Black-throated Green Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Townsend's Warbler (*Setophaga townsendi*)

Some birds have very specific uses for the bryophytes. The Townsend's Warbler (***Setophaga townsendi***; Figure 78) lines its nest with the **setae** (stalks of moss capsules) of mosses (and hair) (Baicich & Harrison 2005).

Figure 78. ***Setophaga townsendi***, Townsend's Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 79. ***Setophaga occidentalis***, Hermit Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Kirtland's Warbler (*Setophaga kirtlandii*)

In Michigan the Kirtland's Warbler (***Setophaga kirtlandii***; Figure 80) harvests moss sporophytes (Brian Dykstra, pers. comm. 10 December 2011).

Figure 80. ***Setophaga kirtlandii***, Kirtland's Warbler, in Jack pine. Members of this species harvest moss sporophytes, presumably for their nests. Photo by Ron Austing, through Creative Commons.

Figure 81. ***Setophaga striata***, Blackpoll Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 82. ***Setophaga cerulea***, Cerulean Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 83. ***Setophaga ruticilla***, American Redstart. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 84. ***Setophaga citrina***, Hooded Warbler. Members of this species use bryophytes in their nests. Photo by Mary Elliott, through Creative Commons.

Figure 85. ***Setophaga citrina***, Hooded Warbler. Members of this species use bryophytes in their nests. Photo by USFSW, through public domain.

Prothonotary Warbler (*Protonotaria citrea*)

The Prothonotary Warbler (***Protonotaria citrea***; Figure 86) nests in abandoned holes made by woodpeckers. Although it sometimes uses few mosses in the actual nest, it does build it on a bed of bryophytes, both mosses and liverworts (Bent 1953; Petit 1989; Blem & Blem 1992, 1994). When building in a nest box, the mosses go in first to form the bed. Then the nest is built on top of them. The bryophytes remain moist, but the cup is not. Blem and Blem found that 75-80% of the dry mass of the nests they studied is composed of mosses and liverworts. They identified five species of mosses and two liverworts (Table 1), with the moss ***Anomodon attenuatus*** (Figure 87) predominating. They suggested that the bryophytes maintain the needed environment within the nest cavity (*e.g.* Mertens 1977a, b). In addition to ameliorating the moisture, bryophytes may serve to reduce pathogens and parasites (Clark & Mason 1985). I have seen several pictures of these nests, but unfortunately I could not find the name of the photographer on those sites.

Figure 86. ***Protonotaria citrea***, Prothonotary Warbler, a species that uses a bed of bryophytes under its nest. Photo by David Inman, through Creative Commons.

Table 1. Occurrence of bryophytes in Prothonotary Warbler (***Protonotaria citrea***) nests in nest boxes along the James River, Virginia, USA. From Blem & Blem 1994.

Species	Percent occurrence Top	Middle	Bottom	Total
Mosses				
Anomodon attenuatus	97.3	96.4	91.4	95.0
Haplocladium microphyllum	20.6	13.4	21.0	18.3
Amblystegium varium	6.7	7.6	1.3	5.2
Plagiomnium cuspidatum	2.7	1.3	3.1	2.4
Thuidium delicatulum	0.4	1.3	0.0	0.6
Liverworts				
Porella platyphylla	21.9	27.3	32.1	27.1
Frullania eboracensis	0.4	0.8	0.8	0.7

Figure 87. ***Anomodon attenuatus*** with capsules, the primary bryophyte used in the nest of the Prothonotary Warbler. Photo by Bob Klips, with permission.

Worm-eating Warbler (*Helmitheros vermivorum*)

The Worm-eating Warbler (***Helmitheros vermivorum***; Figure 88) uses stems of ***Polytrichum*** in its nest (Figure 89) (Baicich & Harrison 2005).

Figure 88. ***Helmitheros vermivorum***, Worm-eating Warbler. Members of this species use bryophytes in their nests. Photo by Jerry Oldenettel, through Creative Commons.

Figure 89. ***Polytrichum commune***, a moss in a genus used in nests of ***Helmitheros vermivorum***, Worm-eating Warblers. Photo by Hermann Schachner, through Creative Commons.

Figure 90. ***Limnothlypis swainsonii***, Swainson's Warbler. Members of this species use bryophytes in their nests. Photo by Carol Foil, through Creative Commons.

Ovenbird (*Seiurus aurocapilla*)

The seclusive Ovenbird (***Seiurus aurocapilla***; Figure 91-Figure 92) may be dependent on mosses in its environment. Apfelbaum and Haney (1981) reported the disappearance of the Ovenbird from a severely burned Jack pine (***Pinus banksiana***; Figure 93-Figure 95) forest in the Great Lakes area. In that fire, ~80% of the feather moss (Figure 96) communities suffered severe loss due to the fire. But other factors related to the fire may have caused them to disappear.

Figure 91. ***Seiurus aurocapilla***, Ovenbird, a ground nester that may be dependent on mosses in its habitat. Photo by Tom Grey, with permission.

Figure 92. ***Seiurus aurocapilla***, Ovenbird, nest and nestlings. Photo by Fredlyfish4, through Creative Commons.

Figure 93. Jack pine (***Pinus banksiana***) healthy forest. Photo by M. Ricon, through Creative Commons.

Figure 94. ***Pinus banksiana*** after fire in Baraga, Michigan, USA. Photo by Janice Glime.

Figure 95. Burned moss in Jack pine forest, Baraga, MI. Photo by Janice Glime.

Figure 96. ***Pleurozium schreberi***, a feather moss that covers vast areas of ground in conifer forests. Photo by Sture Hermansson, with online permission.

Figure 97. ***Parkesia noveboracensis***, Northern Waterthrush. Some members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 98. ***Parkesia motacilla***, Louisiana Waterthrush. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 99. ***Oporornis agilis***, Connecticut Warbler. Members of this species use bryophytes in their nests. Photo from connecticut-warbler-audubon-field-guide, free stock photos.

Figure 100. ***Geothlypis trichas***, Common Yellowthroat. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 101. ***Cardellina pusilla***, Wilson's Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 102. ***Cardellina canadensis***, Canada Warbler. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Furnariidae – Neotropical Ovenbirds

In the Neotropical ovenbirds (**Furnariidae**) moss use in nesting materials seems to have at least somewhat followed evolutionary lines (Zyskowski & Prum 1999). ***Premnoplex brunnescens*** (Figure 103) builds a domed nest of mosses (Figure 104-Figure 106). This nest may be suspended from structures such as logs.

Figure 103. ***Premnoplex brunnescens***, Spotted Barbtail. Members of this species build domed nests of bryophytes. Photo by Murray Cooper, through Creative Commons.

Figure 104. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Juan Ignacio Areta, through Creative Commons.

Figure 105. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Harold Greeney, through Creative Commons.

Figure 106. ***Premnoplex brunnescens***, Spotted Barbtail, nest of bryophytes. Photo by Gustavo Londoño, through Creative Commons.

In the Neotropical ***Cranioleuca albiceps*** group (see Figure 107), ***Margarornis*** (Figure 108-Figure 109), ***Premnoplex brunnescens*** (Figure 103-Figure 106), ***Siptornis*** (Figure 110), and Plain Softtail, (***Phacellodomus fusciceps***; see Figure 111), a "pensile" nest (Figure 109) is constructed (Zyskowski & Prum 1999). This is a large nest with a small brood chamber that is entered from below. It is constructed from top down by draping long strands of green mosses or strips of other plant material. The nest hangs down from a log or rocky overhang and in ***Premnoplex brunnescens*** it may also hang from vines. ***Asthenes*** (Figure 112) species construct an ovoid nest (Figure 113) using fresh ***Sphagnum*** (Figure 114). An outer shell of herbaceous stems loosely surrounds it.

Figure 107. *Cranioleuca pallida*, Pallid Spinetail, in Brazil. Members of the ***Cranioleuca albipes*** group build pensile nests that incorporate bryophytes. Photo by Ciro Albano, through Creative Commons.

Figure 108. ***Margarornis rubiginosus***, Ruddy Treerunner. Members of this species make nests among bryophytes. Photo by Carmelo López Abad, through Creative Commons.

Figure 109. ***Margarornis squamiger***, Pearled Treerunner, pensile nest imbedded in bryophytes and rootlets with an entrance at the bottom. Photo by Harold Greeney, through Creative Commons.

Figure 110. ***Siptornis striaticollis***, Spectacled Prickletail, nest. Photo by Harold Greeney, through Creative Commons.

Figure 111. ***Phacellodomus ruber***, Greater Thornbird. Members of this species construct their nests using mosses and other plant material. Photo by Cláudio Dias Timm, through Creative Commons.

Figure 112. ***Asthenes anthoides***, Austral Canastero, Members of ***Asthenes*** incorporate bryophytes in their nests. Photo by Collaerts brothers, through Creative Commons.

Figure 113. ***Asthenes flammulata,*** Many-striped Canastero nest in Ecuador. Photo by Harold Greeney, through Creative Commons.

Figure 114. ***Sphagnum austinii***, member of a genus used in nests of ***Asthenes***. Stan Phillips, through public domain

White-browed Spinetail (*Hellmayrea gularis*)

In the Andean cloud forests, the White-browed Spinetail (***Hellmayrea gularis***; Figure 115) nests (Figure 116) were embedded in hanging masses of epiphytic mosses, but rather than being pendulous, the nests were supported from below or from the sides by stems (Greeney & Zyskowski 2008). These nests were ball-shaped with a side entrance. The exterior consisted of green moss, whereas the internal side consisted of dry bamboo leaves. The nest was lined with soft materials, either *Tillandsia* seed down (Figure 117) or tree-fern scales (Figure 118).

Figure 115. ***Hellmayrea gularis***, White-browed Spinetail, bringing grub to nest. Photo by Murray Cooper, through Creative Commons.

Figure 116. ***Hellmayrea gularis***, White-browed Spinetail, nest embedded in mosses. Photo by Harry Greeney, through Creative Commons.

Figure 117. *Tillandsia schiedeana*; the down (coma) of seeds in this genus are used in the nests of the White-browed Spinetail (***Hellmayrea gularis***). Photo by Roger Culos, through Creative Commons.

Figure 118. Hairy tree fern frond showing scales and hairs used in nests of the White-browed Spinetail, ***Hellmayrea gularis***. Photo by Janna Schreier <janna@jannaschreier.com>, with permission.

Thraupidae – Tanagers & Honeycreepers

Wolf (2009) found one species of **Thraupidae** that use bryophytes in their nests in North America: ***Piranga ludoviciana*** (Western Tanager; Figure 119).

Figure 119. ***Piranga ludoviciana***, Western Tanager. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Yellow-bellied Dacnis (*Dacnis flaviventer*)

The Yellow-bellied Dacnis (***Dacnis flaviventer***; Figure 120) is a bird of the high canopy and nests in this genus are largely unknown. Sheldon and Greeney (2008) were fortunate enough to find one nest and describe it. Although most of the nest is made of ferns, mosses comprise the sparse lining of the cup, woven with rootlets and dried grasses in a circular fashion.

Figure 120. ***Dacnis flaviventer***, Yellow-bellied Dacnis male. Members of this species line their nests with mosses. Photo by Patty McGann, through Creative Commons.

Emberizidae – Emberizines

Wolf (2009) found thirteen species of **Emberizidae** that use bryophytes in their nests in North America:

Spizella arborea (American Tree Sparrow; Figure 121-Figure 122)
Pooecetes gramineus (Vesper Sparrow; Figure 123-Figure 124)
Ammodramus savannarum (Grasshopper Sparrow; Figure 125-Figure 126)
Passerella iliaca (Fox Sparrow; Figure 127)
Melospiza lincolnii (Lincoln's Sparrow; Figure 128)
Zonotrichia albicollis (White-Throated Sparrow; Figure 129)

Zonotrichia querula (Harris's Sparrow; Figure 130)
Zonotrichia leucophrys (White-Crowned Sparrow; Figure 131-Figure 132)
Zonotrichia atricapilla (Golden-Crowned Sparrow; Figure 133)
Junco hyemalis (Dark-Eyed Junco; Figure 134-Figure 137)
Junco phaeonotus (Yellow-Eyed Junco; Figure 138)
Calcarius lapponicus (Lapland Longspur; Figure 139-Figure 140)
Plectrophenax nivalis (Snow Bunting; Figure 141)

Figure 121. ***Spizella arborea***, American Tree Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 122. ***Spizella arborea***, American Tree Sparrow, nest and nestlings. Photo from USFWS, through public domain.

Figure 123. ***Pooecetes gramineus***, Vesper Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 124. ***Pooecetes gramineus***, Vesper Sparrow, nestlings in nest, begging. Photo by Kati Fleming, through Creative Commons.

Figure 125. ***Ammodramus savannarum***, Grasshopper Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 126. ***Ammodramus savannarum***, female Grasshopper Sparrows in nest. Photo by Janet Ruth, USGS, through public domain.

Figure 127. ***Passerella iliaca***, Fox Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 128. ***Melospiza lincolnii***, Lincoln's Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 129. ***Zonotrichia albicollis***, White-throated Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 130. ***Zonotrichia querula***, Harris's Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 131. ***Zonotrichia leucophrys***, White-crowned Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 132. ***Zonotrichia leucophrys***, White-Crowned Sparrow, nest with eggs. Photo by Jacob W. Franks, NPS, through public domain.

Figure 133. ***Zonotrichia atricapilla***, Golden-crowned Sparrow. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Junco (*Junco hyemalis*)

The common Junco (***Junco hyemalis***; Figure 134) spends its winter in snowy places in the northern USA, then returns to even more northern locations in late April to build its nest of grasses, moss, and rootlets nestled in a mossy bank (Figure 135) or along a woodland trail (Figure 136) (Harrison 2000). Ken-ichi Ueda found a similar construction in a stream bank (Figure 137).

Figure 134. ***Junco hyemalis***, Dark-eyed Junco. Members of this species use bryophytes in their nests. Photo by USFWS, through public domain.

Figure 135. ***Junco hyemalis***, Dark-eyed Junco, nest with eggs in mossy cavity. Photo from USFWS, through public domain.

Figure 136. ***Junco hiemalis***, Dark-eyed Junco, nest with ***Hedwigia ciliata***. Photo courtesy of Susan Studlar.

Figure 137. Junco nest in mossy stream embankment. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 138. ***Junco phaeonotus***, Yellow-eyed Junco. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 139. ***Calcarius lapponicus***, Lapland Longspur. Members of this species use bryophytes in their nests. Photo by Ómar Runólfsson, through Creative Commons.

Figure 140. ***Calcarius lapponicus***, Lapland Longspur, nest. Photo by James K. Lindsey, with permission.

Figure 141. ***Plectrophenax nivalis***, Snow Bunting,. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Eastern Towhee (*Pipilo erythrophthalmus*)

The Eastern Towhee (***Pipilo erythrophthalmus***; Figure 142), formerly the Rufous-sided Towhee, nest (Figure 143) is somewhat unusual in its moss component. The lining can consist of a single material – 70-80 strands of ***Polytrichum ohioense*** setae (Figure 144) interwoven to form the lining (Breil & Moyle 1976). A few had **gametophyte** (leafy plants) fragments or capsules attached.

Figure 142. ***Pipilo erythrophthalmus***, Eastern Towhee male. Members of this species that use setae of ***Polytrichum ohioense*** (Figure 144) to line their nests in the southeastern USA. Photo by Bill Thompson, through Creative Commons.

Figure 143. ***Pipilo erythrophthalmus***, Eastern Towhee, nest. Photo by Bill Thompson, through Creative Commons.

Figure 144. ***Polytrichum ohioense*** showing setae that can be used to line the nests of the Eastern Towhee (***Pipilo erythrophthalmus***). Photo by Bob Klips, with permission.

Savannah Sparrow (*Passerculus sandwichensis*)

Mosses comprised more than 30% of the mass of nesting materials in the southeastern Ontario, Canada, populations of the ground-nesting Savannah Sparrow (***Passerculus sandwichensis***; Figure 145-Figure 146) compared to less than 20% in the northern Manitoba populations (Crossman *et al*. 2011). Although these differences were not statistically significant ($p > 0.05$), they may reflect the somewhat smaller, more compact nests in the northern Manitoba population. But does it vary with climate as an adaptive means to maintain more favorable temperatures? Indeed Crossman and coworkers found that whereas the external dimensions of the nest did not differ, the inner nest cup was significantly shallower in northern Manitoba, indicating a thicker bottom that could provide greater insulation in the northern Manitoba population. But alas, we do not know if the mosses contributed to any insulating properties.

Figure 145. ***Passerculus sandwichensis***, Savannah Sparrow, a species for which moss usage and nest size vary with latitude. Photo by Tom Grey, with permission.

Figure 146. ***Passerculus sandwichensis***, Savannah Sparrow, nest with eggs. Photo by James K. Lindsey, with permission.

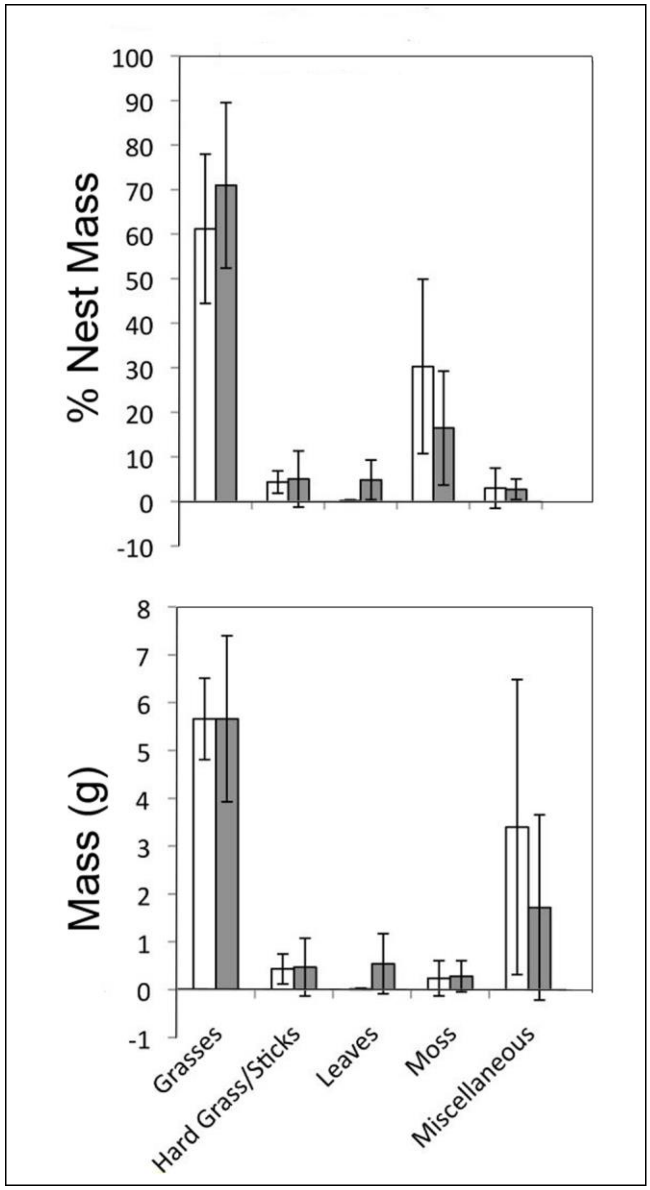

Figure 147. Nest composition for materials comprising ≥1% of nest mass of the Savannah Sparrows (***Passerculus sandwichensis***; Figure 145-Figure 146) that bred in southeastern Ontario (white bars) and northern Manitoba (grey bars). Bars represent dominant nesting materials ≥1% of nest dry mass. Those materials comprising <1% of nest mass are combined into miscellaneous. Plots show means (± SD). Modified from Crossman *et al*. 2011.

Ipswitch Sparrow (*Passerculus sandwichensis princeps*)

The Ipswich Sparrow (***Passerculus sandwichensis princeps***; Figure 148) is endemic on Sable Island, Nova Scotia, Canada. Dwight (1895; Mills & Lucas 2016) notes that mosses are included in their nests. As is typical in many kinds of nests, these are composed of two distinct parts. The outer shell is made of coarse materials including dead weed stalks, grasses, and "little bits" of mosses. The inner cup has finer materials, including hair of ponies and cattle, grasses, and sedges. These nests differ from those of the Savannah Sparrow on the mainland, where the nest is scraped out to form hollows and contain no mosses or lining materials.

Figure 148. ***Passerculus sandwichensis princeps***, Ipswich Sparrow. Members of this subspecies are endemic to Nova Scotia and often include mosses in the linings of their nests. Photo through Creative Commons.

Icteridae – Blackbirds, Orioles, *etc.*

Wolf (2009) found three species of **Icteridae** that use bryophytes in their nests in North America:

Euphagus carolinus (Rusty Blackbird; Figure 149-Figure 150)
Euphagus cyanocephalus (Brewer's Blackbird; Figure 151)
Icterus bullockii (Bullock's Oriole; Figure 152-Figure 154)

Figure 149. ***Euphagus carolinus***, Rusty Blackbird. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 150. ***Euphagus carolinus***, Rusty Blackbird, female on nest. Photo by USFWS, through public domain.

Figure 151. ***Euphagus cyanocephalus***, male Brewer's Blackbird. Members of this species use bryophytes in their nests. Photo by Alan D. Wilson, through Creative Commons.

Figure 152. ***Icterus bullockii***, Bullock's Oriole. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 153. ***Icterus bullockii***, Bullocks Orioles. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 154. Hanging nest of ***Icterus bullockii***, Bullock's Oriole. Members of this species use bryophytes in their nests. Photo by Eugene Zelenko through Creative Commons.

Fringillidae – Fringilline Finches

Wolf (2009) found eleven species of **Fringillidae** that use bryophytes in their nests in North America:

Leucosticte tephrocotis (Gray-crowned Rosy Finch; Figure 155)
Leucosticte atrata (Black Rosy Finch; Figure 156)
Leucosticte australis (Brown-capped Rosy Finch; Figure 157)
Pinicola enucleator (Pine Grosbeak; Figure 158)
Carpodacus purpureus (Purple Finch; Figure 159-Figure 160)
Loxia curvirostra (Red Crossbill; Figure 161)
Loxia leucoptera (White-winged Crossbill; Figure 162)
Carduelis flammea (Common Redpoll; Figure 163-Figure 164)
Carduelis pinus (Pine Siskin; Figure 165)
Carduelis psaltria (Lesser Goldfinch; Figure 166-Figure 167)
Coccothraustes vespertinus (Evening Grosbeak; Figure 168)

Figure 155. ***Leucosticte tephrocotis***, Gray-crowned Rosy Finch, in British Columbia. Members of this species use bryophytes in their nests. Photo by Nigel, through Creative Commons.

Figure 156. ***Leucosticte atrata***, Black Rosy Finch, in British Columbia. Members of this species use bryophytes in their nests. Photo by Peter Wallack, through Creative Commons.

Figure 157. ***Leucosticte australis***, Brown-capped Rosy Finch. Members of this species use bryophytes in their nests. Photo by Dominic Sherony, through Creative Commons.

Figure 158. ***Pinicola enucleator***, Pine Grosbeak. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 159. ***Carpodacus purpureus***, Purple Finch. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 160. ***Carpodacus purpureus***, Purple Finch, feeding young in nest. Photo by Robert Kuhn <www.theonlinezoo>, through Creative Commons.

Figure 161. ***Loxia curvirostra***, Red Crossbill. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Figure 162. ***Loxia leucoptera***, White-winged Crossbill male. Members of this species use bryophytes in their nests. Photo by John Harrison, through Creative Commons.

Figure 163. ***Carduelis flammea***, Cock Redpoll. Members of this species use bryophytes in their nests. Photo by Gail Hampshire, through Creative Commons.

Figure 164. ***Carduelis flammea***, Common Redpoll, feeding young in nest. Note mosses woven into the exterior. Photo by Peter Reese, through nzbirdsonline.org.nz, online permission.

Pine Siskin (*Carduelis pinus*)

The Pine Siskin (***Carduelis pinus***; Figure 165) breeds from SE Alaska to Newfoundland (Van Woerkom 1999). They remain year-round along the Pacific Coast where they prefer coniferous forests and mixed woodlands. Their nests are saucer-shaped, constructed with twigs, grasses, strips of bark, and lichens. These are lined with hair, moss, thistledown, or feathers. The young leave the nest in two weeks. The female remains in the nest with the young and the male brings food for her and she regurgitates food for the nestlings.

Figure 165. ***Carduelis pinus***, Pine Siskin. Members of this species use bryophytes in their nests. Photo by Cephas, through Creative Commons.

Figure 166. ***Carduelis psaltria***, Lesser Goldfinch male. Members of this species use bryophytes in their nests. Photo by Gail Hampshire, through Creative Commons.

Figure 167. ***Carduelis psaltria***, Lesser Goldfinch female. Members of this species use bryophytes in their nests. Photo by Alan D. Wilson, through Creative Commons.

Figure 168. ***Coccothraustes vespertinus***, Evening Grosbeaks, getting drink. Members of this species use bryophytes in their nests. Photo by Tom Grey, with permission.

Brambling (*Fringilla montifringilla*)

The Brambling (***Fringilla montifringilla***; Figure 169) has a name that literally means "mountain fringilla" (Wikipedia 2016a) It lives in birchwoods and coniferous forests of northern Europe and Asia. It is migratory, overwintering in southern Europe, north Africa, north India, northern Pakistan, China, and Japan. This small passerine bird uses mosses, hair, and wool to line its nest (Stevenson 1987).

Figure 169. ***Fringilla montifringilla***, Brambling. Members of this species use bryophytes in their nests. Photo by M. Nishimura, through Creative Commons.

Chaffinch (*Fringilla coelebs*)

Based on the pictures I have seen, the Chaffinch (***Fringilla coelebs***; Figure 170) commonly uses bryophytes extensively in its nests (Figure 171-Figure 173).

Figure 170. ***Fringilla coelebs***, Chaffinch female. Members of this species use bryophytes in their nests. Photo by James K. Lindsey, with permission.

Figure 171. ***Fringilla coelebs***, Chaffinch, nest made largely of bryophytes. Photo by James K. Lindsey, with permission.

Figure 172. ***Fringilla coelebs***, Chaffinch, nest with extensive use of bryophytes. Photo by Trachemys, through Creative Commons.

Figure 173. ***Fringilla coelebs***, Chaffinch, nest of bryophytes. Photo by Nottsexminer, through Creative Commons.

Poo-uli (*Melamprosops phaesoma*)

The Poo-uli (***Melamprosops phaeosoma***; Figure 174) is a Hawaiian honeycreeper, a rare species nearing extinction (Engilis *et al*. 1996;). Its nest is an open cup which it constructs from twigs and bryophytes. Coarse mosses are used to fill the spaces between the twigs, reminiscent of human uses of mosses for chinking. Both nests examined contained ***Homaliodendron flabellatum*** (Figure 175), ***Thuidium plicatum***, ***Trachypodopsis auriculata*** (Figure 176). One nest also contained ***Aerobryopsis wallichi***; the other contained ***Floribundaria floribunda*** (Figure 177). The lining is made from fern rootlets. Leaves and stems of graminoids and dicots constituted less than 5% of the material in the nest.

Figure 174. ***Melamprosops phaeosoma***, Poo-uli, a rare species. Members of this species use bryophytes in their nests. Photo by Paul E. Baker, through public domain.

Figure 175. ***Homaliodendron flabellatum***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo by Yao, through Creative Commons.

Figure 176. ***Trachypodopsis auriculata***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo through Creative Commons.

Figure 177. ***Floribundaria floribunda***, a species used in the nest of the Poo-uli, ***Melamprosops phaeosoma***. Photo through Creative Commons.

Kākāwahie or Moloka'i Creeper (*Paroreomyza flammea*)

Kākāwahie or Moloka'i Creeper (***Paroreomyza flammea***; Figure 178) is an extinct member of this family, originally native to Hawaii (Wikipedia 2016b). It fed primarily on larvae of beetles and Lepidoptera. The birds constructed a nest with an exterior of moss.

Figure 178. ***Paroreomyza flammea***, Moloka'i Creeper (bottom 2 birds), an extinct bird that placed mosses on the exterior of the nest. Photo by Frederick William Frohawk, through Creative Commons.

Leiothrichidae – Laughing Thrushes

Nilgiri Laughing Thrush (*Trochalopteron cachinnans*)

The Nilgiri Laughing Thrush (***Trochalopteron cachinnans***; Figure 179) gathers bryophytes and uses them to build nests. These typically include several species.

Figure 179. ***Trochalopteron cachinnans***, Nilgiri Laughing Thrush. Members of this species use bryophytes in their nests. Photo by Antony Grossy, through Creative Commons.

Ptilonorhynchidae – Bower Birds

Bower Birds have some of the most interesting mating behavior in the bird world. The male bower bird builds a mating tunnel or similar structure to attract his mate (Hansell 2000). This tunnel typically involves a column of sticks around a stem of a sapling or small fern that serves

as a central feature of the bower. Depending on the species, this bower is often decorated with blue objects.

Vogelkop Bowerbird (*Amblyornis inornata*)

The Vogelkop Bowerbird (***Amblyornis inornata***; Figure 180) of New Guinea and Australia builds a conical hut (Figure 181) up to 2 m wide by 3.3 m high (Uy 2002). The pathway to this doorway of this hut is paved with a carpet of moss. This mossy path is decorated with rhododendron flowers, red ginger berries, iridescent blue beetle carapaces, and feathers from other birds. One isolated population in the Kumawa Mountains builds a spire around saplings, forming an umbrella-like structure over a circular mossy foundation.

Figure 180. ***Amblyornis inornata***, Vogelkop Bowerbird. Members of this species pave the pathways to their huts with mosses. Photo by Carmelo López Abad, through Creative Commons.

Figure 181. ***Amblyornis inornata***, Vogelkop Bowerbird, bower with hut. Photo by Carmelo López Abad, through Creative Commons.

The females of the Vogelkop Bowerbird (***Amblyornis inornata***; Figure 180) are slightly smaller than the males (Lananhbirds 2010). The dull coloration is offset by one of the largest and most colorful bowers. The bower is a 100-cm-high cone with a 160-cm diameter. Like many human homes, the birds have a front lawn that is cleared and carpeted with mosses. The lawn is the site of flowers, fruit, beetle wings, dead leaves, and other objects in an "artistic" arrangement. Males maintain these objects, replacing ones that are no longer suitable or replacing ones stolen by neighbors.

Because of the dull plumage, this species is of less interest than other Bowerbird species and therefore is of Least Concern on the IUCN Red List (BirdLife International 2004). That is, if humans don't like it, they don't hunt it for its plumage.

Macgregor's Bowerbird (*Amblyornis macgregoriae*)

The Macgregor's Bowerbird (***Amblyornis macgregoriae***; Figure 182) contrasts with the Vogelkop Bowerbird by having the "simplest" bower (Hansell 2000). It builds a maypole tower that is 2-3X the height of the male. This is made of a few hundred fine, interlocked sticks in the center of a moss platform. The platform lacks other adornment.

Figure 182. ***Amblyornis macgregoriae***, Macgregor's Bowerbird. Members of this species use bryophytes in their nests. Photo by Katerina Tvardikova, through Creative Commons.

Golden-fronted Bowerbird (*Amblyornis flavifrons*)

The Golden-fronted Bowerbird (***Amblyornis flavifrons***) builds a bower similar to that of Macgregor's Bowerbird, but the lawn is decorated by little piles of yellow, green, and fruit (Hansell 2000).

Acanthizidae – Scrubwrens, Thornbills, and Gerygones

The Brown Thornbills (***Acanthiza pusilla***; Figure 183) are very active birds, searching for tiny invertebrates (Lloyd 2013). They make an untidy nest (Figure 184)of bark shreds, grass, spider webs, spider egg sacs, amd moss. This nest is hidden close to the ground in tussock grass, saggs or bracken.

Figure 183. ***Acanthiza pusilla*** (Brown Thornbill), a bird that includes mosses in its nest. Photo by Patrick Kavanagh, through Creative Commons.

Figure 184. ***Acanthiza pusilla*** (Brown Thornbill) nest that often includes mosses. Photo by J. J. Harrison, through Creative Commons.

Rhinocryptidae – Tapaculos

Silvery-fronted Tapaculo (*Scytalopus argentifrons*)

In a Costa Rican cloud forest, the nest of the Silvery-fronted Tapaculo (***Scytalopus argentifrons***; Figure 185) was a "substantial" globular structure (Young & Zuchowski 2003). It was made mostly of mosses placed into a subterranean cavity at the end of a short, narrow tunnel.

Figure 185. ***Scytalopus argentifrons***, Silvery-fronted Tapaculo, Members of this species put mosses in their underground nests. Photo by Francesco Veronesi, through Creative Commons.

Callaeatidae – New Zealand Wattlebirds

The Kōkako (***Callaeas wilsoni;*** Figure 186), endemic to the North Island of New Zealand, sometimes includes moss capsules to line its nest (Figure 187). They use lichens, mosses, and liverworts, together with rotten wood and some mud in a central layer of the nest (Jessica Beever, Bryonet 2 May 2003).

Figure 186. ***Callaeas wilsoni***, Kōkako, a New Zealand endemic species. Members of this species use moss capsules to line their nests. Photo through Creative Commons.

Figure 187. ***Callaeas wilsoni***, Kōkako, in a nest with lots of mosses. Photo by Dick Veitch, © Department of Conservation, NZ, with limited online permission.

Zosteropidae – White-eyes

The White-eye (***Zosterops lateralis***; Figure 188-Figure 189) builds a nest (Figure 190) with mosses on the outside (Wikipedia 2017). This tiny nest is suspended from a fork in the branches.

Figure 188. ***Zosterops lateralis***, Wax-eye, a bird that cloaks the outside of its nest in mosses. Photo by Phil Bendle, with permission.

Figure 189. ***Zosterops lateralis***, White-eye. Photo by fir002, through Creative Commons.

Figure 190. ***Zosterops lateralis***, White-eye nest with mosses. Photo by Phil Bendle, with permission.

Effect of Cavity-nesting Birds on Bryophyte Communities

We have already discussed dispersal of bryophytes by birds, but nesting birds can have other effects on bryophyte communities as well. Tatsumi *et al*. (2017) investigated the effects of birds on the tree bole surrounding cavities where birds have nested (Figure 191-Figure 194). They suggested that tree holes (Figure 195-Figure 198) that are inhabited can be enriched with nutrients from those organisms, and those nutrients can escape down the tree trunk. Using the trees *Aria japonica* and *Cercidiphyllum japonicum* in a Japanese temperate forest, they investigated the bryophyte and lichen communities above and below tree holes.

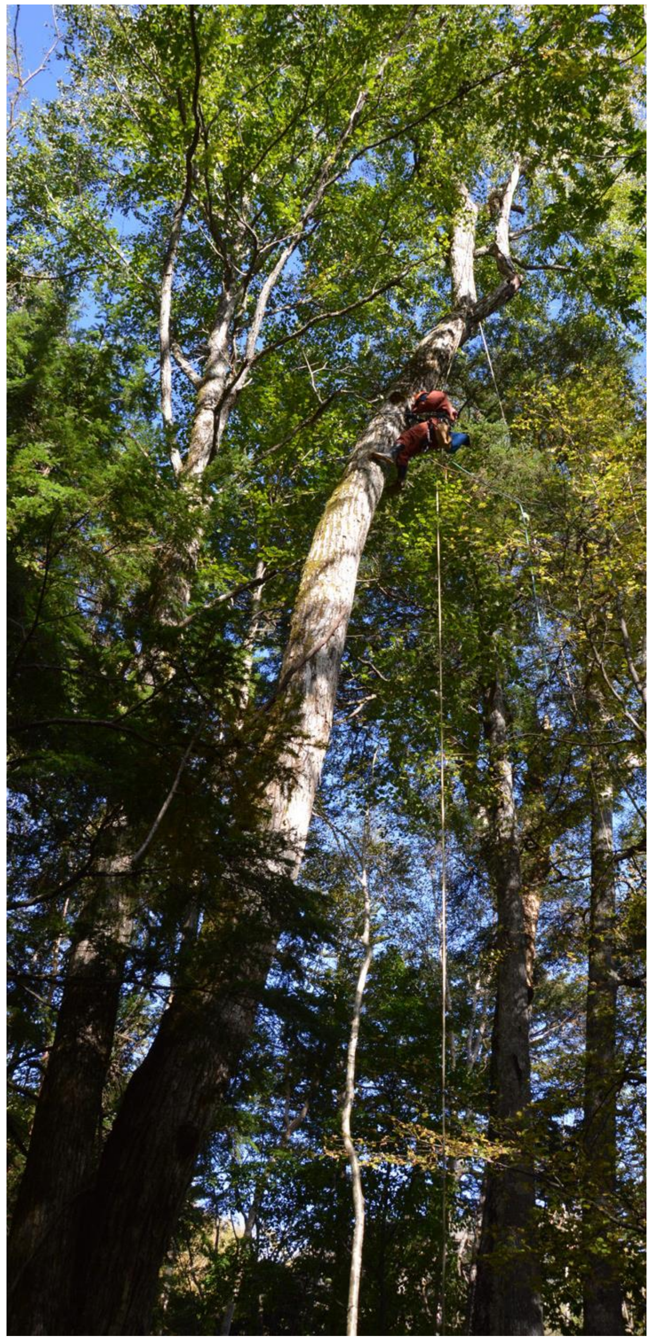

Figure 191. Scaling large trees to investigate the tree hole nesters. Photo courtesy of Shinichi Tatsumi.

Figure 192. Tree hole methods – one of the researchers prepares to place a quadrat frame. Photo courtesy of Shinichi Tatsumi.

Figure 193. Tree hole methods, with a quadrat positioned above the tree hole. Photo courtesy of Åsa Ranlund.

Figure 194. Tree hole methods showing quadrat below the tree hole. Photo of courtesy of Yume Imada.

Figure 195. Tree hole showing diversity above and below the hole. Photo courtesy of Wakana Azuma.

Figure 196. Elongate tree hole and climbing equipment. Photo courtesy of Wakana Azuma.

Figure 197. View of inside of tree hole. Photo courtesy of Wakana Azuma.

Figure 198. Close view of tree hole vegetation. Photo courtesy of Shinichi Tatsumi.

The richness of bryophyte and lichen species did not differ above and below the tree holes (Tatsumi *et al*. 2017). But the species composition of bryophytes differed significantly. The moss ***Anomodon tristis*** (Figure 199) and liverwort ***Porella vernicosa*** (Figure 200) were significantly more common below than above tree holes. On the other hand, the liverwort ***Radula japonica*** (Figure 201) and four lichen species were more frequent above than below the holes. Tatsumi and coworkers suggested nutrient and moisture differences as possible reasons for the species differences. I have to wonder how much the activity of the parents going in and out of the cavity could affect the bryophytes surviving there. These could have two impacts, dispersal and damage. More fragile species might not be able to survive the activity. Others might be transported there on feathers and feet.

Figure 199. ***Anomodon tristis***, a moss that is more common below tree holes than above. Photo by Bob Klips, with permission.

Figure 200. ***Porella vernicosa***, a liverwort that is more common below tree holes than above. Photo by Masanobu Higuchi, with permission.

Figure 201. ***Radula japonica***, a liverwort that is more common above tree holes than below. Photo by Taiwan Mosses, through Creative Commons.

Edible Nests

An interesting twist to the food concept is the use of bird nests as food for humans. I have not documented that any of those used contain mosses, but Salgado *et al*. (1998) found mosses in neotropical bird nests that they examined for **zoopharmacognosy** (behavior in which non-human animals apparently self-medicate by selecting and ingesting or topically using plants, soils, insects, or psychoactive drugs to prevent or reduce harmful effects of pathogens and toxins).

Summary

These passerine birds use mosses for a variety of purposes in their nests. Some put them inside as liners, some make the bottom of the nest thicker, and some weave them on the outside as camouflage. But in most cases we don't know what the function of the mosses really is – insulation, moisture, camouflage, or parasite protection. Or could it be all of these, or simply the mosses are the most available building materials?

The choice of bryophytes usually seems to depend on availability. But in other cases, the species chooses particular bryophytes, even if they are less abundant. Some bowerbirds use mosses to decorate their bowers – making a green path to the nest.

Birds can have an impact on the bryophytes themselves. Aside from being destructive by removing the bryophytes, and dispersing them to new locations, they have an impact on the species found above and below the tree holes where they nest.

Acknowledgments

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