

CHAPTER 16-1

BIRDS AND BRYOPHYTES INTERSECT

TABLE OF CONTENTS

Where Birds and Bryophytes Intersect.....	16-1-2
Watch Towers and Sentinels.....	16-1-3
Bathing.....	16-1-4
Thirsty Birds.....	16-1-5
Fertilizer Effects of Birds on Bryophytes.....	16-1-5
Guano.....	16-1-7
Penguins.....	16-1-10
Peatland Habitats.....	16-1-10
Effects on Bryophyte Community Structure.....	16-1-16
Conservation Issues.....	16-1-17
Dispersal Agents.....	16-1-18
Soft Landings.....	16-1-23
Summary.....	16-1-23
Acknowledgments.....	16-1-23
Literature Cited.....	16-1-23

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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.

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.



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.

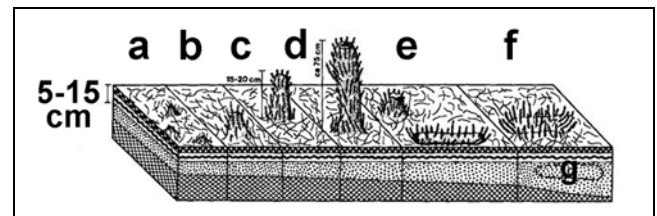


Figure 4. Developmental stages of bird watchtowers made of bryophytes. **a.** moss hummocks among morasses; **b.** early developmental stage of tower; **c.** immature tower; **d.** tower at optimum development stage; **e.** tower after collapse; **f.** collapsed tower overgrown by *Polytrichum* shoots;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

Spending time on these towers detracts from the time spent foraging and thus is a tradeoff (Metcalfé & 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 (Metcalfé 1984; Sullivan 1984).

Hollén *et al.* (2008) demonstrated that in the Pied Babbler (*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 23. Guano of gulls and puffins on Farne Islands. Photo by Matthew Wills, through Creative Commons.



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



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

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 **ornithocrophilous** 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 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.

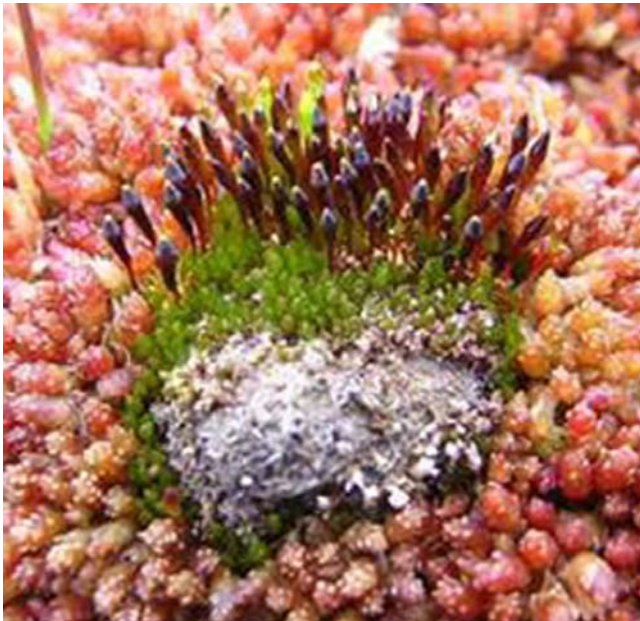


Figure 33. *Tayloria dubyi* with capsules, a species that lives on bird dung, especially of the Upland Goose, in the subAntarctic Magallanes ecoregion. Photo by Jocelyn Jofré, through Creative Commons.



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 Taylor, 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 $\delta^{15}\text{N}$ signatures (>15%), indicating their use of animal-derived N through repeated trophic transfer by microbial activity since the original deposition.



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

In the case of the Adélie 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 (*Leiostyris 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 (*Zenaidura 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 48. *Carduelis tristis*, American Goldfinch, a species that commonly occurs in bogs during breeding season. Photo by MDF, 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 49. *Empidonax traillii*, Willow Flycatcher, a species that commonly occurs in bogs during breeding season. Photo by Dominic Sherony, 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 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 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 52. *Bombycilla cedrorum*, Cedar Waxwing, a species that commonly occurs in bogs during breeding season. Photo by Cephas, through Creative Commons.



Figure 55. *Toxostoma rufum*, Brown Thrasher, a species that commonly occurs in bogs during breeding season. Photo by E. Monk, 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 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 crane fly *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 crane fly 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 indicator 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 m², 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 Pahi, *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 Beaver 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. Felicísimo *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.

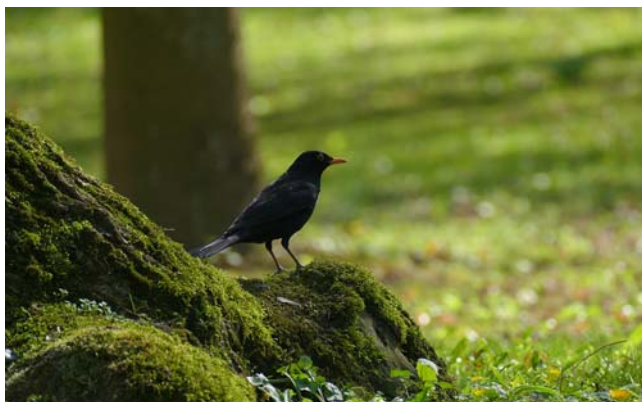


Figure 97. Bird on moss perch – Is it a sentinel, or just cooling its feet on the moss? Photo by Ervin Gjata, through public domain.

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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