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CHAPTER 7-2
ARTHROPODS: ARACHNIDA – SPIDER BIOLOGY

TABLE OF CONTENTS

CHAPTER 7-2
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Figure 1. ***Arctosa*** *cf*. ***alpigena*** female on moss, showing disruptive coloration that makes it more difficult to see. It has been reported from mosses in more than one study (Harvey *et al.* 2002; Almquist 2005). Photo by Walter Pfliegler, with permission.

SUBPHYLUM CHELICERATA

The subphylum **Chelicerata** includes the spiders and mites, both having members associated with bryophytes. Both spiders and mites are in the class **Arachnida**, along with scorpions, harvestmen, ticks, and Solifugae. The **Chelicerata** are characterized by four pairs of walking legs, a pair of chelicerae, and a pair of pedipalps. Although the arachnids are not as small as many of the organisms in preceding chapters, many are small enough that the bryophytes still provide sufficient space for many of these taxa to navigate easily among the stems and leaves. Hence, we should expect to find the bryophytes to be a suitable habitat for a number of these.

Following the concept of a niche, bryophytes can provide a number of important "resources" for arachnids. The most obvious of these are shelter and protection. With **disruptive coloration** on their backs, spiders and other small arachnids can hide among the bryophytes undetected by would-be predators such as birds. This shelter may provide a safe site when an arachnid is being chased or provide a protected niche for an egg case during incubation. The protection also extends to anchorage and shelter from wind, diffusion of raindrops (avoiding the impact of a free-fallen drop), temperature buffering, and retention of humidity. Further possibilities include having a place to lie in wait for a walking meal to meander by, or perhaps even eating the bryophyte itself, a menu item that is poorly documented (and unlikely) for spiders.

But bryophytes may also extend their benefits to those arachnids not living among the branches. Bryophytes help to keep the soil beneath humid, soft, and pliable for longer periods than that experienced by bare soil. They permit an arachnid to emerge from a burrow and look around while remaining hidden beneath a canopy of loose bryophytes. Even those arachnids traversing the surface of bryophytes may benefit from the disruptive coloring of mosses that make the disruptive colors of arachnid backs less conspicuous. Or they may simply add a place where humidity is greater, helping arachnids to travel greater distances before risk of drying. And who knows if these arachnids might take advantage of the early morning dew captured by bryophyte leaves to gain a drink of water.

With all these possibilities, we would expect some arthropods to have distinct adaptations to that bryophytic habitat. Indeed some do, but I feel certain many stories remain to be discovered.

Class Arachnida

The arachnids include the spiders (order **Araneae**), mites (subclass **Acarina**), ticks (subclass **Acarina**), and harvestman or daddy-long-legs (order **Opiliones**). These are creatures that somewhat resemble insects, but as adults they have eight legs. They have one or two main body regions, not three as in insects. Among these, the mites are fairly common residents in moss clones. Although the other arachnids are not very common among bryophytes, there are, nevertheless, some interesting stories about all of these inhabitant groups.

Arachnid Trapping Limitations

Little quantitative work exists for any arachnids except that for the moss-dwelling mites. One limitation that might suggest that bryophytes are unimportant is the typical sampling method used for forest floor arthropods, including arachnids. Pitfall traps are typically used for those arthropods that are active above the surface during some part of the 24-hour cycle (Curtis 1980). But if arthropods spend most of their time within the bryophyte mat rather than on the surface, they are not likely to fall into such traps.

Curtis found that responses of spider species to four pitfall trapping methods differed, causing distortions in the community species frequency curves. Hence, we should expect even greater differences among a wider range of methods. For example, Komposch (2000) studied the spiders in wetlands of Austria using pitfall traps, light traps, soil sifters, and hand collections. As will be seen in studies cited in this chapter, this broader set of methods gets better representation of groups like the **Linyphiidae**, a very species-rich family of small spiders with many species living among bryophytes.

Pitfall traps are sunken into the ground with water or other liquid to trap the fallen arthropods. The top is covered with a wide mesh screen to keep out debris and possesses a second raised cover to keep rain out. The container can be simple, like a cereal bowl (Figure 2) or can (Figure 3). Although bait is shown in the diagrams, it is not necessary and may introduce a bias if the study is quantitative.

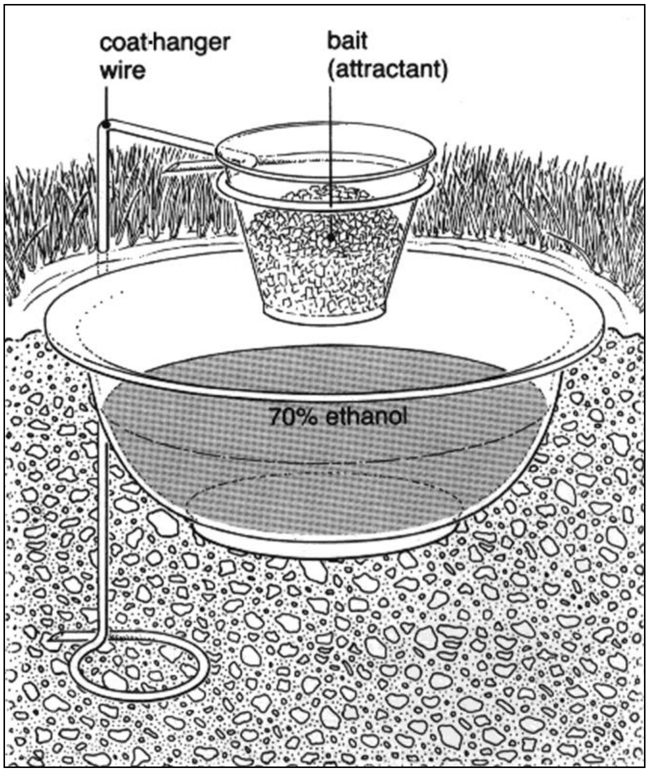

Figure 2. Pitfall trap with cereal bowl holding alcohol. The bait will bring the organisms to the trap, but most will fall into the alcohol before reaching the wire that gives them access. Drawing from USDA website.

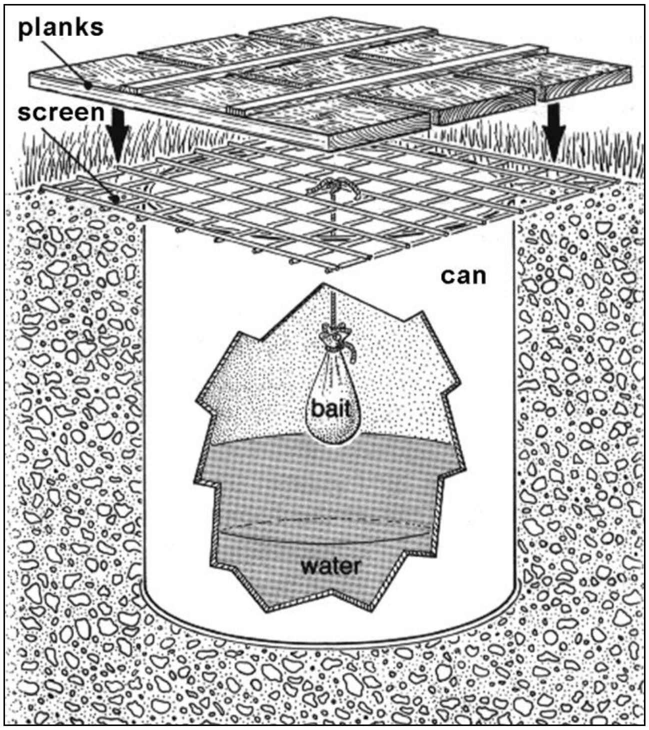

Figure 3. Pitfall trap using a can with water to trap arthropods. Drawing from USDA website.

In the tropics, fogging with pesticides (Pyrethrin) can reveal a number of canopy arthropod fauna. However, most of the bryophyte dwellers remain trapped within the bryophyte clumps (Yanoviak *et al*. 2003). The smaller ones, like the **Linyphiidae,** are the least likely to drop from the canopy into the collecting containers, giving a biased representation of the community and even missing some species entirely.

Such trapping limitations tend to limit the habitat descriptions of spider fauna. For example, Koponen (1999) described the fauna of the Finnish taiga, but only mentioned the mosses ***Pleurozium schreberi***, ***Dicranum***, and ***Hylocomium splendens*** as the dominant ground cover without relating the spider locations to them.

Sieving might be a somewhat better technique for bryophyte dwellers, but for many species that live among the branches of the mosses, only hand picking is likely to uncover some of the species sufficiently to represent their abundance. We need to examine the efficacy of typical trapping and other sampling methods on enumeration of bryophyte-dwelling arthropods.

Order Araneae – Spiders

"*Once upon a time Anansi the Spider was walking, walking, walking through the forest when something caught his eye. It was a strange moss-covered rock. "How interesting!" Anansi said. "Isn't this a strange moss-covered rock!*" (Kimmel 1988).

Kimmel (1988) uses mosses and a spider to build a children's story. In this story, a spider uses "strange moss-covered rock" to trick the other animals, but Little Bush Deer decides the spider needs to learn a lesson.

Spiders in nature use mosses to provide cover and camouflage against predation. Rocks with mosses are indeed interesting, although not quite in the way of trickery that Anansi used them. They house many kinds of arthropods, spiders among them.

Nomenclature for spiders follows Platnick (2000-2013).

Spider Biology

There are approximately 40,000 species of spiders in the world (Wikipedia 2012a; InsectIdentification 2013). Spiders are 8-legged creatures that have chitinous coverings and two body regions, the **cephalothorax** (head and thorax as one external unit) and abdomen. Unlike the insects, they lack antennae. Instead, they have various hairs that penetrate their chitinous covering (Wikipedia 2010d). Some of these may be sensitive to the slightest movement, such as that of wind. Others are sensitive to chemicals, thus achieving the role of insect antennae and our noses and tongues.

The legs originate on the underside of the cephalothorax. Instead of muscles, they use hydraulic pressure to extend their legs, although they have muscles to flex them. This explains why dead spiders always have the legs drawn in – no pressure to extend them. And any puncture to the chitin of the cephalothorax causes loss of water pressure and certain death.

Spiders have chelicerae (claws) with fangs that they use to inject venom into their forthcoming dinner. Most of these poisons are not serious dangers for humans, although they can cause itching or painful swelling locally. Only one herbivorous spider is known (Meehan *et al*. 2009), all others being predators. Therefore, we should not expect them to consume bryophytes.

Spiders excrete uric acid, a very concentrated form of nitrogen waste, thus permitting them to conserve water for long periods of time. This reduction of need for water may help to explain their reticence to live among mosses where humidity is often high, but there are at least some spiders that live in the water, so one would expect some to be adapted to the higher humidity of bryophytes in other habitats.

While bogs probably host the majority of spider species associated with bryophytes, many spiders live among bryophytes also in drier habitats. Humid forests are often rich in bryophytes. But dry habitats such as coastal dunes may also have a high coverage of bryophytes serving as habitats for spiders, even though these bryophytes are dried up much of the time.

Although at times the Linyphiidae may be somewhat numerous, in other cases spiders are a minor component of the bryophyte habitat. In the epiphyte mats of Costa Rican cloud forests, where bryophytes are only one component, Yanoviak *et al*. (2007) found spiders among the lowest in representation among 10 groups of arthropods, occupying about 1% of the fauna in the cloud forests in the wet season and 1-2% in the dry season.

Growth Forms and Life Forms

Bryophytes are often lumped together as if they are all the same to their animal communities, but growth and life forms can make quite a difference to the living space within. Gimingham and Birse (1957) related growth form response to decreasing levels of moisture, from dendroid and thalloid mats in high moisture to short turfs and cushions in low moisture. Vilde (1991) showed that differences in life form can reduce evaporative rate by 5.3-46 times, depending on the species and site conditions.

The two terms of **life form** and **growth form** have been confused in the literature (La Farge 1996), as discussed in Chapter 4-5. To reiterate briefly here, **growth** form is a purely morphological term and although genetically determined, it can be modified by the environment, as opposed to **life form**, which is more encompassing and describes the result of life conditions, including growth form, influence of environment, and assemblage of individuals (Warming 1896; Mägdefrau 1982). La Farge-England (pers. comm. 1996) sums it up by stating that **life form** is the **assemblage** of individual shoots, branching pattern, and directions of growth as modified by the habitat, whereas **growth form** is a property of an **individual**, the structures of the shoots, direction of growth, length, frequency and position of branches.

Mägdefrau (1969) defined the following **life forms**, to which I have added examples and habitats:

annuals: ***Phascum***, ***Riccia*** – disturbed habitats
short turf: ***Trichostomum brachydontium***, ***Barbula*** – epiphytes; tundra
tail: ***Prionodon densus***, ***Leucodon***
cushion: ***Leucobryum*** – deciduous & conifer forests; epiphytes; alpine; desert
mat: ***Hypnum***; ***Plagiothecium*** – moist forests; conifer forests; epiphytes; alpine; tundra
fan: ***Neckeropsis*** – humid tropical forests; epiphytes
tall turf: ***Dicranum*** spp.; ***Polytrichum*** – conifer forests; alpine; tundra

weft: ***Hylocomium***, ***Pleurozium*** – conifer & deciduous forests; desert; alpine; tundra
dendroid: ***Climacium***, ***Hypnodendron*** -
pendant: **Meteoriaceae** – humid tropical forests; epiphytes

Sphagnum does not fit well into these categories because of its loose interior with an expanded apex. It perhaps most closely fits into the tall turf.

A comparison of these categories as spider habitats may provide interesting relationships. However, few studies address the moisture benefits of various life forms to the bryophytes and none seem to address this question experimentally for the spiders. Therefore, we can only theorize. Life forms will be mentioned occasionally throughout this chapter, but they should be viewed with some caution because the vocabulary used seems to be primarily confined to mat vs cushion.

Bryophytes as Cover

As early as 1896, Banks recognized the importance of mosses for spiders, including the **Linyphiidae** ***Eridantes*** (as *Lophocarenum*) ***erigonoides***, ***Islandiana flaveola*** (as *Tmeticus flaveolus*), and ***Scylaceus*** (as *Tmeticus*) ***pallidus*** in moss on Long Island, NY, USA. Bryophytes form important cover for many kinds of spiders. Es'kov (1981) found that an abundant moss cover is important for spider populations in the Russian taiga; Vilbaste (1981) likewise found spider fauna in mires of Estonia. Diverse invertebrate bryophyte communities similar to those found in the soil are common in the tundra (Chernov 1964), so it is possible that the bryophyte habitat is an important feeding area for spiders there. Bonte *et al*. (2003) found a significant correlation between spiders and moss cover in the coastal grey dunes along the North Sea. Larrivée *et al*. (2005) found a correlation between spiders and moss/lichen cover in burned areas, but not in clearcut areas, suggesting that the two types of deforestation elicit very different responses from the spider populations.

Pearce *et al*. (2004) compared the microhabitats of spiders in boreal forests of northwestern Ontario, Canada. They found that among the four stand types, spiders did not view mosses as simply mosses. Rather, ***Agyneta olivacea*** (see Figure 4; **Linyphiidae**) and ***Pardosa uintana*** (see Figure 22; **Lycosidae**) occupied microhabitats associated with feather mosses (wefts; Figure 5) rather than those of ***Sphagnum*** (tall turf; Figure 6), suggesting the possibility that life or growth form may be important.

Figure 4. Male ***Agyneta ramosa*** on a moss, giving one an idea of its small size. Photo by Jørgen Lissner, with permission.

Figure 5. ***Hylocomium splendens***, a weft-forming feather moss. Photo by Michael Lüth, with permission.

Figure 6. ***Sphagnum russowii***, where a variety of spiders might take advantage of the humidity. Photo by Michael Lüth, with permission.

Among the few studies to consider the bryophyte habitat specifically, that of Biström and Pajunen (1989) compares the fauna in two forest locations in southern Finland. In these forests, they considered the fauna on ***Polytrichum commune*** (Figure 7) and several species of ***Sphagnum*** (Figure 6). They found seven generalist spiders, all **Linyphiidae** [***Centromerus arcanus*** (Figure 16), ***Dicymbium tibiale*** (Figure 8), ***Semljicola faustus*** (as *Latithorax faustus*; Figure 9), ***Lepthyphantes alacris*** (Figure 10), ***Minyriolus pusillus*** (Figure 11-Figure 12), ***Tapinocyba pallens*** (Figure 13), and ***Walckenaeria cuspidata*** (Figure 14)], that occurred with these mosses at all five of the main collecting sites during the May to October collecting season.

Figure 7. ***Polytrichum commune***, a moss with a measureable cuticle. Photo by Des Callaghan, with permission.

Figure 8. ***Dicymbium tibiale*** on mosses. Photo by Jørgen Lissner, with permission.

Figure 9. ***Semljicola faustus*** female. Photo by Jørgen Lissner, with permission.

Figure 10. ***Lepthyphantes alacris***, one of the common spiders associated with bryophytes in forests of Finland. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 11. ***Minyriolus pusillus*** male on mosses. Photo by Jørgen Lissner, with permission.

Figure 12. ***Minyriolus pusillus*** male on ***Polytrichum***, a small generalist spider that is common among forest mosses of Finland. Photo by Jørgen Lissner, with permission.

Figure 13. ***Tapinocyba pallens*** male on moss. Photo by Jørgen Lissner, with permission.

Figure 14. ***Walckenaeria cuspidata*** female on moss. Photo by Jørgen Lissner, with permission.

Drozd *et al*. (2009) sampled under moss "cushions" and in litter, obtaining 55,000 invertebrate specimens. They found that the arthropod association, including spiders, reflects interaction between presence of mosses (***Polytrichum commune***, ***Polytrichastrum formosum***, ***Sphagnum teres***, ***Bazzania trilobata***, ***Pleurozium schreberi***, ***Eurhynchium angustirete***, ***Oligotrichum hercynicum***) and other features of the microhabitat. Moss presence, moss species, and moisture are very important characters for both total arthropod abundance and abundance of various arthropod groups. On the other hand, the total arthropod abundance and that of most groups is actually higher in the litter than in moss cushions (*p* = 0.0003). Although the surface activity is considerable, the dense moss cushion prevents them from moving effectively or with due speed. Hence the larger arthropod taxa avoid the dense interior by staying on the surface.

Trampling

Few studies on trampling effects on bryophytes or on spiders exist. Nevertheless, one can imagine that anything that squashes the spaces where spiders move about in search of food would have a negative impact on the spider community. Duffey (1975) studied the effects of trampling on invertebrates in grassland litter and found that the air space dropped from 63% to 38% as a result of 10 treads per month. Although there was little difference in the invertebrate fauna between two levels of trampling, there was significant reduction in the spider fauna. Furthermore, spiders were sensitive at a much lower trampling level than the vegetation itself. It is possible that spiders living among bryophytes would suffer similarly from compaction. On the other hand, it could be that the bryophytes would spring back, offering patches of refuge following trampling of other vegetation. This would make an interesting study.

Abundance, Richness, and Specificity

Quantitative studies are not as common as species richness studies, but one can, nevertheless, find a number of studies with species numbers. For our purposes, however, it is difficult to identify which of those species is associated directly with bryophytes rather than just occurring in a habitat that has bryophytes.

In the study by Biström and Pajunen (1989) in two forest locations in southern Finland, there were 23 species that occurred in at least one of the main sites with a density of at least one individual per square meter. At Borgå they found approximately 57 species associated with ***Polytrichum commune*** (Figure 7), some of which were juveniles and could not be identified to species. In association with ***Sphagnum girgensohnii*** (Figure 15) they found only 43 species. ***Centromerus arcanus*** (Figure 16) and **Erigoninae** juveniles were among the most abundant at both sites. The most abundant of bryophyte-associated species, ***Centromerus arcanus*** (Figure 16), is only 1.5-2.6 mm long (Roberts 1987) and exhibited mean densities of 8.7-24.4 individuals per square meter (Biström & Pajunen 1989). Somewhat less abundant were ***Dicymbium tibiale*** (1.8-11.9 mm; Figure 8) and ***Lepthyphantes alacris*** (0.7-2.0 mm; Figure 10).

Figure 15. ***Sphagnum girgensohnii***, a common woodland species. Photo by Michael Lüth, with permission.

Figure 16. ***Centromerus arcanus***, the most abundant spider associated with ***Sphagnum*** in a Finish study. Photo by Jørgen Lissner, with permission.

I found the greater number of species associated with ***Polytrichum commune*** (Figure 7) (Biström & Pajunen 1989) to be somewhat surprising because the ***Polytrichum*** species do not have the high moisture-holding capacity available with species of ***Sphagnum*** (Figure 15). Perhaps the ***Polytrichum commune*** is too dry for some spiders, as suggested by the moisture data of Biström and Pajunen (1989), but for others some of the wetter mosses are less desirable. Too much water can affect the ability to exchange gasses through the tiny spider tracheae, causing the spiders to drown. ***Polytrichum commune*** provides a high spot out of the wet environment. It would be interesting to monitor the behavior of the spiders as water levels change in the bog and fen ecosystems. Such moisture and morphological differences are not exclusionary for most of the generalist spiders, but may be of importance in the distributions of rarer species.

I also wonder which of these mosses provides a habitat where maneuverability is greater. It would appear to me that it would be easier to move among ***Sphagnum*** stems (Figure 15) than among those of ***Polytrichum commune*** (Figure 7), but perhaps the spider does not perceive it that way. It would be interesting to experiment with the environmental variables vs the morphological characters that differ among these species to see just what factors are important to the location of the spiders. One must also consider the possibility of sampling bias. Although the sieve technique used by the researchers in this study seems to be the most appropriate for bryophytes, it may have differed in effectiveness between moss genera.

No spider species seemed to be especially abundant on just one bryophyte species and rare on the others, suggesting that they either had relatively wide tolerances for the conditions available or that they were sufficiently mobile to be found in the range of species locations due to transit between preferred sites. For example, some species of the **Linyphiidae** subfamily **Erigoninae** may be numerous in an area one day and gone the next (Wikipedia 2010b). This lack of specificity is consistent with observations by Graves and Graves (1969) in North Carolina, USA. They found no habitat specificity for the spiders among mosses, fungi, *Rhododendron* leaf litter, and other microhabitats.

Isaia *et al.* (2009) present us with a very useful study from the Abruzzo Apennines in Central Italy. They used a Berlese apparatus to extract spiders from "wet" mosses.

Not surprisingly, the **Linyphiidae** were the most prominent family. This is a large family of tiny spiders and was represented by 22 of the 38 species.

In all, Isaia and coworkers (2009) found 494 spiders among wet mosses from the Apennines in Central Italy, representing 38 species in 36 genera and 14 families, an interesting distribution where lack of multiple species in the same genus suggests niche separation. Some were more generalists, occurring in mosses and elsewhere [***Robertus lividus*** (Figure 17-Figure 18; **Theridiidae**), ***Caracladus leberti*** (**Linyphiidae**), ***Diplocephalus arnoi*** (*cf*. Figure 19; **Linyphiidae**), and ***Antistea elegans*** (Figure 20; **Hahniidae**)]. Juveniles of ***Lepthyphantes*** (Figure 10), ***Parachtes***, ***Cryphoeca*** (Figure 21), ***Pardosa*** (Figure 22), ***Pirata*** (Figure 23), and ***Xysticus*** (Figure 24), all rather common genera, likewise included the mosses among their habitats.

Figure 17. ***Robertus lividus*** female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 18. ***Robertus lividus***. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 19. ***Diplocephalus latifrons*** male on moss, a spider sometimes associated with bryophytes. Photo by Jørgen Lissner, with permission.

Figure 20. ***Antistea elegans***, a known moss dweller. Photo by Jørgen Lissner, with permission.

Figure 21. ***Cryphoeca silvicola***, a species whose young have been found among mosses in the Abruzzo Apennines of Central Italy (Isaia *et al*. 2009). Photo by Glenn Halvor Morka, with permission.

Figure 22. ***Pardosa monticola***, representing a genus with moss-dwelling members. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 23. ***Pirata piraticus***, a moss-dwelling spider. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Figure 24. ***Xysticus cristatus*** (ground crab spiders), member of a genus known from mosses. Photo by Trevor & Dilys Pendleton <www.eakringbirds.com>, with permission.

Parachtes siculus (**Dysderidae**) prefers wet places, so mosses proved to be a suitable place for this species (Isaia *et al*. 2009). Not surprisingly, they found a new species of **Linyphiidae** (***Diplocephalus arnoi***) from wet mosses, with 96 out of 103 specimens from mosses associated with the film of water on rocks (**petrimadicolous** mosses). ***Mecopisthes latinus*** (**Linyphiidae**) also occurred among these mosses. The **Hahniidae** in wet mosses were represented by ***Antistea elegans*** (Figure 20), the most abundant, followed by immature members of ***Cryphoeca*** (Figure 21). One male of ***Cryphoeca silvicola*** (Figure 21) could be identified, and one male of ***Hahnia ononidum*** (Figure 25), known elsewhere from mosses, as well as ***Ozyptila claveata*** (or possibly ***O. trux***?) (see Figure 26; **Thomisidae**) from wet mosses. This small number of males may be an artifact due to their smaller size and greater difficulty of finding them.

Figure 25. ***Hahnia ononidum*** female. Photo by Glenn Halvor Morka, with permission.

Figure 26. ***Ozyptila trux*** on ***Plagiomnium*** sp. This genus is sometimes represented on or among wet mosses. Photo by Glenn Halvor Morka, with permission.

Moisture Relationships

Many spiders are particularly prone to desiccation, whereas some species from arid climates are able to survive without water for months and even years. Entling et al. (2007) found that spider β-diversity was strikingly higher in open habitats than in forests, suggesting that they have either behavioral or physiological means to protect them from desiccation. Many spiders are night-active, permitting them to enter more exposed areas without the danger of desiccation from daytime sun. Anyone who has put a living spider in a jar knows that spiders easily dehydrate, leading to their death. Their legs contract due to the loss of hydrostatic pressure.

But in a study of five species of spiders from various habitats, Vollmer and MacMahon (1974) could find no relationship with habitat. Likewise, Gajdo and Toft (2000), using pitfall traps, found no relationship between epigeic spiders and moisture in a heathland-marsh gradient in Denmark. In the latter case, the habitat ranged from 100% cover of mosses to near zero.

Rather, body size seemed to be a better determinant of the rate of water loss (Vollmer & MacMahon 1974), with small spiders losing moisture more rapidly due to their larger surface area to volume ratio. This water loss leads to reduced survivorship in smaller individuals (Vincent 1993).

One adaptation for survival of these small species and individuals is behavioral – living among bryophytes or taking periodic refuge there. As will be seen in many of the examples in this chapter, bryophyte-dwelling spiders are frequently small.

On the other hand, the critical activity point does correlate with the moisture of the habitat (Vollmer & MacMahon 1974), suggesting that bryophytes may permit spiders, especially small ones, to be more active.

Nonetheless, DeVito *et al*. (2004) found that within the spider genus ***Pardosa***, distribution did indeed follow a moisture gradient related to a stream. But even these were not restricted by proximity to the shoreline. Bruun and Toft (2004) were able to demonstrate a moisture gradient in two Danish peat bogs, with ***Pardosa sphagnicola*** (Figure 27-Figure 29) and ***Oedothorax gibbosus*** (Figure 30) at the moist end of the gradient and ***Haplodrassus signifer*** (Figure 31) and ***Zelotes*** spp. (Figure 32) at the dry end. They concluded that moisture and vegetation density were the determining factors for community composition.

Figure 27. ***Pardosa sphagnicola*** on mosses. Photo by Walter Pfliegler, with permission.

Figure 28. ***Pardosa sphagnicola*** female with egg sac. Photo by James K. Lindsey, with permission.

Figure 29. ***Pardosa sphagnicola*** female with young spiderlings. Photo by James K. Lindsey, with permission.

Figure 30. ***Oedothorax gibbosus*** female on ***Sphagnum***. Photo by Jørgen Lissner, with permission.

Figure 31. ***Haplodrassus signifer*** male on moss. Photo by Jørgen Lissner, with permission.

Once we understood the mechanisms of water loss by spiders, size became a logical explanation. The **tracheae** are the respiratory organs where oxygen enters the body (Davies & Edney 1952). Thus they are also exit points for water, but also cause drowning if too much water is present to block them. Humphreys (1975) pointed out that water loss is influenced by the size of the spider, temperature, saturation deficit, and by relative humidity per se. Davies and Edney demonstrated that up to 30°C the rates of water loss in mg cm^{-3} hr^{-1} were low, never more than 1.6 (dead spiders with free spiracles) and usually <0.6.

Figure 32. ***Zelotes latreillei***. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Hence, temperature is also important in conserving moisture. Animals exposed at 2°C intervals from 40-50°C show a steep rise in water loss starting at 42°C (Davies & Edney 1952). The species are ordered by critical temperatures (lowest to highest): *Zygiella* (as *Zilla*) *atrica* [outsides of houses (Emerton 1902); woodlands (Elton 1928)], ***Pardosa amentata*** (Figure 45; **Lycosidae**; bogs), ***Metellina segmentata*** (as *Meta*) [Figure 33; **Tetragnathidae**; some species in breaks in blanket bogs (Cherrett 1964)]; *Tegenaria domestica* (as *T. derhami*) [wooded areas, deserts, coastal areas, grassy fields, inside man-made structures (Hunt 2012)]. *Zygiella* (as *Zilla*) *x-notata* [outsides of houses (Emerton 1902); woodlands (Elton 1928)] shows a less defined critical temperature and a lower rate of evaporation than any other study species at higher temperatures. Experiments with dusting caused a six-fold increase in the evaporation rate of ***Pardosa amentata***, causing Davies and Edney (1952) to conclude that a wax layer might be present in the cuticle. Since living organisms lost water more slowly than dead ones, it is likely that this cuticle is secreted by living organisms. There are no experimental data on bryophyte-dwelling spiders and any cuticular relationship relative to temperature.

Figure 33. ***Metellina segmentata***. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

In the Morr House National Nature Reserve, Westmorland, GB, Cherrett (1964) found ***Metellina*** (as *Meta*) ***merianae*** (Figure 34; **Tetragnathidae**) and ***Larinioides*** (as ***Araneus***) ***cornutus*** (Figure 35-Figure 36; **Araneidae**) only in breaks in the blanket bog (Cherrett 1964). ***Metellina merianae*** was mostly in peat overhangs, suggesting that it was avoiding either sun (heat, light) or finding a moist site that was open enough for easy movement. Cherrett attributed this distribution to avoidance of light. Four other species, however, were distributed in a way suggesting they had the ability to withstand desiccation.

Figure 34. ***Metellina merianae***. Photo by Glenn Halvor Morka, with permission.

Figure 35. ***Larinioides cornutus*** spiderling, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.

Figure 36. ***Larinioides cornutus*** female, an inhabitant of blanket bogs. Photo by James K. Lindsey, with permission.

I don't know of any direct observations of spiders drinking water from mosses, but I consider it likely that it occurs. The water in soil capillary spaces provides a source of water, even for the larger Lycosidae. Parry (1954) experimented with ***Alopecosa*** (as *Tarentula*) ***barbipes*** (Sundevall), a species of heathlands and one of the larger British lycosids, and *Hogna* (as *Lycosa*) *radiata*. Parry demonstrated that when these spiders had lost about 10% of their normal weight, they would nearly always take advantage of an opportunity to drink from these capillary spaces. It would seem that water adhering in the capillary spaces of bryophytes would be even easier to obtain than that within the soil and may be an important source of water in places such as sand dunes. ***Alopecosa barbipes*** occurs on calcareous coastal dunes in Flanders, Belgium, where the ground cover is predominately mosses (***Syntrichia ruralis***, ***Hypnum cupressiforme*** var. ***lacunosum***), low grasses, and low herbs (Bonte *et al.* 2000). The mosses in this habitat may be important as a source of drinking water.

Importance of Temperature

We have seen the importance that temperature holds for two lycosid spiders living on and in the ***Sphagnum*** mat. In geothermal areas, bryophytes often form the dominant vegetation. Studies of spiders living there may produce new records, or at the very least, range extensions, but a search with Google Scholar produced nothing on this relationship.

But spiders also inhabit cool areas. Růžička and Hajer (1996) found that spiders in North Bohemia lived on mountain tops and peat bogs as well as on the lower edges of boulders where the air stream created "an exceedingly cold microclimate." They found ***Diplocentria bidentata*** (Figure 37; **Linyphiidae**) in pitfall traps laid among mosses at the edge of the stony debris. ***Semljicola*** (as ***Latithorax***) ***faustus*** (Figure 9; **Linyphiidae**), a species known previously only from peat bogs, and ***Theonoe minutissima*** (Figure 38; **Theridiidae**), also a known bog dweller, occurred in moss at the lower edge of the debris.

Figure 37. ***Diplocentria bidentata*** on moss. Photo by Jørgen Lissner, with permission.

Figure 38. ***Theonoe minutissima*** female on moss. Photo by Jørgen Lissner, with permission.

Temperature can be important at the microclimate scale for nest and web site selection. Riechert and Tracy (1975) showed that there was an 8-fold increase in obtaining energy for *Agelenopsis aperta* (**Agelenidae**), a desert spider, from selection of a favorable thermal environment, compared to only 2-fold for selecting for greater numbers of prey. This is at least partly due to the increased spider activity in more favorable temperatures. Riechert (1985) suggested that shade might provide a cue to sites with favorable temperatures, whereas olfactory and vibratory cues help them to locate prey.

Humphreys (1975) showed that for *Geolycosa godeffroyi* (**Lycosidae**) water loss was a function of temperature. Humphreys suggested that this burrowing spider might be able to obtain water in the soil when it was greater than 11% by using heat differentials as a source of water, even though the spider was unable to extract it from near-saturated air. This heat differential extraction would seem to be a possibility among mosses as well.

The need for temperature optimization can cause spiders to select certain vegetational attributes. In a sagebrush community, spiders selected the most dense foliage form that had been experimentally modified by tying the branches together (Hatley & Macmahon 1980). The species diversity and number of **guilds** (any groups of species that exploit same resources, or that exploit different resources in related ways) were greater there. Should we expect a similar relationship for the scaled down community of small spiders that live among bryophytes? If so, we might expect the communities to differ based on bryophyte life forms.

Hygrolycosa rubrofasciata (**Lycosidae**; Figure 39), a forest species, may choose its habitat for conditions conducive to attracting a mate. The male makes its mating "call" by drumming its abdomen on dry leaves, hence making the bog habitat unsuitable (Kotiaho *et al*. 2000). Kotiaho and coworkers found a positive correlation between dry leaves and presence of spiders. Furthermore, the drumming rate and both male and female mobility were correlated with temperature.

Figure 39. ***Hygrolycosa rubofasciata*** on moss. Photo by Arno Grabolle, with permission.

Food Sources

If you have wondered how those spiders in your cellar find food to survive the winter, perhaps they don't need any, at least for a long time. Forster and Kavale (1989) found that the Australian redback spider (*Latrodectus hasselti*) can survive more than 300 days as adults with no food. Their longevity is greatest at 10°C, making your cellar or cool attic a suitable place to wait out the low food period. This suggests that within a bryophyte mat such spiders could survive a long winter without danger of death by starvation. Apparently most spiders can recover after 2-3 months with no food.

Reports on bryophytes as food for arachnids are relatively rare, although some recent studies have demonstrated that at least some mite taxa consume them (See Chapt 9-1). One suggestion that appears frequently in the literature is that bryophytes either have too little nutritional value, or that it is too difficult to extract that nutritional value from cells that have a large ratio of cell wall (cellulose) to cell contents. But for the arachnids, both the mouth parts and the digestive systems are adapted to eating animal prey.

Spiders may trap their prey or actively hunt for them. Many have poisons that anaesthetize or kill the prey. For example, the **Thomisidae** have their first two pairs of legs modified for grabbing the prey (Lissner 2011a). Their third and fourth legs help to anchor the spider to its substrate during the ensuing, but short, struggle. Once the spider has the opportunity to bite the prey, the prey dies within seconds from the highly potent venom. The longer first two pairs of legs permit the spider to walk sideways like a crab, albeit slowly (Stewart 2001).

Prey size is important to spiders. Whereas they are able to eat captured prey that is larger than they are, this is not necessarily their preferred prey size. Nentwig and Wissel (1986) found that the preferred size ranged 50-80% the size of the spider. Only two of the thirteen spiders in the experiments accepted prey (crickets) that were double their size. Nentwig (1989) found that season had little or no effect on prey size selection. Rather, the important influences were properties of the web, microhabitat, physiological, and behavioral differences among the spider species.

Hunting spiders can be **polyphagous**, feeding on a wide range of prey, or **oligophagous**, specializing on few kinds of organisms (Nentwig 1986). The **monophagous** species are rare, but their single food choice is usually a selection from only a few prey taxa – ants, bees, termites, and other spiders.

Despite the size relationships, the relationship between predator and prey may be unimportant in habitat choice. In one dune system, the relationship between dwarf spiders and their **Collembola** (springtail) prey seems to be a matter of common microhabitat preferences (Bonte & Mertens 2003). In this habitat that experiences severe microclimate fluctuations, both predator and prey aggregate. Both groups are negatively affected by grass coverage, but rather aggregate as a function of moss coverage and not of soil moisture.

Some spiders choose to live among the mosses in trees. When Miller *et al*. (2007, 2008) found a correlation between bryophytes, **Collembola** (springtails), and spiders in Maine, USA, they suggested that spiders depended on the **Collembola** living among the bryophytes for food. When the bryophytes were lost due to gap harvesting of the forest, the arthropod communities were affected, with various responses among the members. Height on the tree influenced the communities (Wagner *et al*. 2007). Bryophytes were most abundant near the tree base. At that level they primarily housed **Acari** (mites), **Araneae** (spiders), and **Collembola**, whereas at 2 m the Diptera (flies) were the most abundant. Loss of trees, and consequent loss of tree-base mosses, resulted in loss of **Collembola** and subsequent reduction in food for spiders.

Other organisms housed among bryophytes are also important as spider food. Among these are **earthworms**. Although predation of spiders on **earthworms** has rarely been observed (Figure 40), it appears that those spioders that do choose these as part of their diet are the ones that live on the ground in leaf litter, moss-covered patches, and under stones and logs (Nyffeler *et al*. 2001). These **earthworms** have a high protein content (~60-70%, dry weight) (MacDonald 1983; Lee 1985) that complements the typical insect diet of spiders. In the non-web-building genus ***Xysticus*** (Figure 41; **Thomisidae**), a crab spider only 7 mm long was able to consume parts of an **earthworm** of 2 cm length (Nyffeler 1982). This was no doubt possible because of the powerful front legs and a potent venom. Even web-building spiders feed on earthworms (Nyffeler *et al*. 2001). These include those making sheet webs (*e.g.* ***Amaurobius*** – **Amaurobiidae**) and silk tubes (*e.g.* ***Atypus*** – **Atypidae**) (Nyffeler *et al.* 2001), both bryophyte dwellers (Blackwell 1857).

By reviewing the literature, Nyffeler *et al*. (2001) found that members of eleven different families of spiders are known to feed on other spiders. As you might expect, these predators belong mostly to larger species (>10.0 mm) that live near the ground in woodlands and grasslands. Among these are species that live in and under clumps of mosses.

Figure 40. ***Leptorhoptrum robustum*** male, a spider that is known from mosses, eating worm. Photo by Jørgen Lissner, with permission.

Figure 41. ***Xysticus cristatus*** among mosses. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Reproduction

Spider mating can be hazardous for the males. Females are usually larger than males, sometimes much larger (Wikipedia 2012a). Hence, males are easily overcome and can serve as dinner for the female. Males, on the other hand, express a number of complex courtship rituals that help them avoid predation by the females. They usually manage to have several matings, being limited by their short two-year life span (but much longer in some species like the tarantula).

Most spiders build nests where they deposit their eggs (Figure 42), often numbering around 1000 (Biodiversity Explorer 2012). When the eggs are expelled, they become surrounded in a viscous liquid that cements the eggs together when they dry (Figure 43). The female provides them with a fluffy silk that covers and insulates them, and she attaches this to vegetation or includes it in her web. This cocoon also serves as protection against ant predation. Eggs laid in summer usually hatch in 1-2 weeks, whereas those laid at the end of summer will over-winter and hatch the following spring or summer. **Lycosidae** (wolf spiders) carry the cocoon attached to the rear of the abdomen (Figure 44) and later carry their young around on their backs (Figure 45), presumably providing further protection.

Figure 42. ***Xysticus ulmi*** (**Thomisidae**) female with eggs among mosses. Photo by Jørgen Lissner, with permission.

Figure 43. *Ero* sp. cocoon, showing attachment. Photo by Walter Pfliegler, with permission.

Figure 44. ***Pardosa pullata*** (**Lycosidae**) female, a bog dweller, on ***Sphagnum***, carrying egg sac on her abdomen, as is typical in her family, Lycosidae. Photo by Jørgen Lissner, with permission.

Figure 45. ***Pardosa amentata*** female with spiderlings. Photo by James K. Lindsey, with permission.

In the **Thomisidae**, no webs or retreats are used for oviposition (Figure 42; Lissner 2011c). The males are much smaller and darker than the females. During courtship, males touch the female in a way that causes her to recognize him as a male spider and she assumes a submissive posture. Once eggs are produced, the female guards the egg sack. Members of the genus ***Xysticus*** (Figure 41) are known from bryophytes (Isaia *et al.* 2009).

Some spiders use mosses as the substrate for depositing their cocoons. Hajer *et al.* (2009) found that ***Theridiosoma gemmosum*** (Figure 46; **Theridiosomatidae**) maintained its egg sac (Figure 47) on ***Hypnum cupressiforme*** (Figure 48) during their study. Alexander (2003) found this spider species among fen vegetation in Cornwall, UK, where it presumably deposits its cocoons. This species has a rather unusual mating behavior. The male releases silken threads between successive copulations (Hajer *et al.* 2009, 2011). The females unwind these draglines, then roll them into a bundle which they ingest before copulating again. Hence this nuptial gift transfers nutrients from the male to the female. Barrows (1918) reported that this species can "always" be found among wet mosses on cliff faces and other wet situations in deep woods.

Figure 46. ***Theridiosoma gemmosum*** adult male on moss. Photo by Jørgen Lissner, with permission.

At least some members of the **Linyphiidae** are known to care for their young by providing food (Willey & Coyle 1992). On the other hand, they may eat their own eggs, at least in captivity – a phenomenon that has rarely been reported for spiders and may not exist in nature. The even smaller size of the young may dictate the need for a more protective environment, *i.e.*, buffered against temperature and moisture fluctuations, during the "child-rearing" period of their lives.

Figure 47. ***Theridiosoma gemmosum*** egg cocoon. Photo by Jørgen Lissner, with permission.

Figure 48. ***Hypnum cupressiforme***. Photo by David Holyoak, with permission.

Scotina celans (Figure 49; **Liocranidae**) lives in both mosses and detritus in woodlands, where it makes a funnel tube for its nest, lying in wait there for prey (Harvey *et al.* 2002). Females regurgitate food to feed the young.

Figure 49. ***Scotina celans*** (**Liocranidae**) on mosses. Photo by Morten D. D. Hansen, with permission.

Nests and Webs

Among the potential uses of bryophytes, some spiders may choose them as a nesting site. This can be a home for the adult who, in most families, lies in wait for its prey. The spider has a unique set of structures called **spinnerets** that produce the silken thread used for making the webs and nests (Figure 50). These webs can be funnels (Figure 51), 3-d structures (Figure 52), or the more commonly figured sheet structures (Figure 53) such as those seen in Halloween decorations. The common moss dwellers in the **Linyphiidae** make horizontal doily webs, sometimes covering large areas (Figure 54-Figure 55). ***Frontinella***, (**Linyphiidae**) the bowl and doily spider, makes an upper bowl-shaped web and a lower, flattened web (Figure 56). The spider rests under the bowl (Figure 57), above the doily, to await prey. ***Eresus sandaliatus*** (Figure 58; **Eresidae**) is one of those that will at least at times use mosses as a location for its food web (Figure 59).

Figure 50. ***Achaearanea riparia*** (**Theridiidae**), occasional moss-dweller (Logunov *et al*. 1998), showing silken thread from spinnerets. Photo by Glen Peterson, through Creative Commons.

Figure 51. This nest of ***Amaurobius ferox*** (**Amaurobiidae**) provides evidence that mosses can be used for its housing. Photo by James K. Lindsey from <www.commonaster.eu>, with permission.

Figure 52. Three-dimensional spider-web. Photo ©<www.free-images.org.uk>, with permission.

Figure 53. Sheet spider web with dew drops. Photo by Fir0002/Flagstaffotos through Wikimedia Commons.

Figure 54. Doily webs of **Linyphiidae**. These occupied over 1000 m^2 in California, USA. Photo by John A. Basanese through Creative Commons.

Figure 55. Doily webs of **Linyphiidae**. Photo by John A. Basanese through Creative Commons.

Figure 56. ***Frontinella*** (**Linyphiidae**) bowl and doily web with spider on under side of web. Some species of ***Frontinella*** occur on mosses. Photo ©Gary Vallé, with permission.

Figure 57. ***Frontinella*** (**Linyphiidae**) spider on under side of bowl part of bowl and doily web. Photo ©Gary Vallé, with permission.

Figure 58. ***Eresus sandaliatus*** (**Eresidae**) male among mosses. Photo by Jørgen Lissner, with permission.

Figure 59. ***Eresus sandaliatus*** (**Eresidae**) food web among bryophytes and lichens. Photo by Jørgen Lissner, with permission.

In the southern part of its range, ***Atypus affinis*** (Figure 60-Figure 62; **Atypidae**) is a rare spider (Jonsson 1998), sometimes building its tubes under mosses with the opening in the mosses. Using a sieving technique, Jonsson was able to distinguish the actual locations of the spiders. He found 90 nest tubes in just one square meter on the tops and sides of stony screes in southern Sweden, often among mosses. These tubes serve as traps for food items. Prey items fall into the trap and are captured and eaten by the spider attacking them from beneath. Only young spiderlings and males ever leave the tube, the males only in search of a female.

Figure 60. ***Atypus affinis*** (**Atypidae**) among grasses, most likely a male in search of a female tube. Photo by Manuel Valdueza through public domain.

Figure 61. ***Atypus affinis*** (**Atypidae**) eggs and spiderlings. Only the spiderlings and female-searching males leave the tube. Photo by Jørgen Lissner, with permission.

Figure 62. ***Atypus affinis*** (**Atypidae**) male. The male in this image is the exoskeleton of a dead male that has been eaten by the female. Photo by Jørgen Lissner, with permission.

In the genus ***Arctosa*** (Figure 1; **Arctosidae),** these medium to large spiders make burrows in mosses, sand, detritus, or under stones (Figure 63) (Lissner 2011c). But some spiders do not make any sort of retreat (Lissner 2011c). The **Thomisidae** make no webs or retreats for any purpose.

Figure 63. ***Arctosa cinerea*** (**Lycosidae**) digging burrow, which members of the genus sometimes do among mosses. Photo copyright by Evan Jones, Spider Recording Scheme/British Arachnological Society (2012) Website and on-line database facility <http://srs.britishspiders.org.uk>.

Hahniidae live close to the ground and construct their small sheet webs among mosses as well as other areas that exhibit small depressions (Lissner 2011b). ***Hahnia nava*** (Figure 64), a sheet-web maker, places its nets in mosses and other low plant forms (Harvey *et al.* 2002). ***Hahnia helveola*** even makes its webs in pine needles, as well as leaf litter, mosses, and low plant forms.

On the southern Appalachian peaks, USA, the tiny size (3-4 mm) of the endangered spruce-fir moss spider ***Microhexura montivaga*** (Figure 65; **Dipluridae**) permits it to live in flattened tube webs under mosses and litter mats of the spruce-fir forests (Coyle 1985). ***Microhexura montivaga***, the smallest of the tarantulas, was first discovered in North Carolina (USFWS 2012). It lives in high elevation remnants of Fraser fir and red spruce forests on shaded boulders exclusively within mats of damp, well-drained mosses and liverworts (Geatz 1994). Its 2-3 mm size permits it to move easily among the branches. Springtails within the moss mats may serve as a primary food source (USFWS 2012). The spider is endangered because its spruce-fir habitat is being destroyed by the balsam woolly adelgid (Hemiptera) (Geatz 1994; Tarter & Nelson 1995; Smith & Nicholas 1998). This canopy destruction results in drying of the mosses, making them unsuitable for this spider.

Figure 64. ***Hahnia nava***, a sheet-web maker that places its webs among mosses and other low vegetation. Photo by Glenn Halvor Morka, with permission.

Figure 65. The moss spider ***Microhexura montivaga*** (**Dipluridae**). Photo by Joel Harp, US Fish & Wildlife Service.

Spiders that live above ground typically produce a security thread by which they can relocate to their webs. It would be interesting to see if this is done among bryophyte-dwelling spiders.

In some cases, the bryophyte seems to play an important role that cannot be served as well as the tracheophyte counterparts. This role is in helping to form the trap door of the trapdoor spiders (Moggridge 1873) including **Ctenizidae** and **Liphistiidae** (Wikipedia 2014) and the lesser known **Cytraucheniidae** (Eiseman & Charney 2010). ***Cyclocosmia torreya***, known primarily from Guatemala, Thailand, and China, builds burrows in moss banks along the Apalachicola River in Florida, USA (Wikipedia 2014). ***Stasimopus mandelai*** (Ctenizidae; see Figure 66), in the Eastern Cape Province of South Africa, makes its trap door of silk and soil with a very light covering of moss (Hendrixson & Bond 2004).

Figure 66. ***Stasimopus robertsi*** at the entrance of its burrow. Another spider in this genus, ***S. mandelai*** incorporates mosses in a trapdoor that covers its burrow. Fritz Geller-Grimm through Creative Commons.

Bits of bryophytes are often added to the door as camouflage (Cloudsley-Thompson 1989), but based on images on the web, growing mosses often comprise part of the lid and appear to help in holding the lid together (Figure 67-Figure 69). The spider hides beneath the lid, and when it sees a prey organism, it darts out from the protective lid to grab the prey. It would seem that a tracheophyte would be too heavy to serve as a network to hold this door together.

Figure 67. Trapdoor spider ***Liphistius malayanus*** (**Liphistiidae**), from China, Japan, and Southeast Asia, under a moss-covered trapdoor. Photo by Amir Ridhwan, Malaysian Spider website, through Creative Commons.

Figure 68. Trapdoor spider (**Ctenizidae**) with bryophytes surrounding it and covering the "door." Photo by Hankplank through Creative Commons.

Figure 69. Trapdoor for the spider ***Hebestatis*** sp. (**Ctenizidae**) under moss. Photo by Marshal Hedin through Creative Commons.

Dormant Stages

One might find a greater site selectivity for the immobile dormant or egg stages. For spiders whose cocoons are not incorporated into the web constructed for trapping prey, the web/feeding site may have very different characteristics from that of the oviposition site (Suter *et al*. 1987). Suter *et al*. (1987) examined the site selection of the linyphiid ***Frontinella communis*** (as *F. pyramitela*) (Figure 56, Figure 70-Figure 71). This species, as far as I know, does not typically use mosses, but the female deposits her eggs in a loosely woven cocoon on or near the soil, whereas many members of this family deposit their eggs aerially where the humidity is usually much lower. It appears that the ***Frontinella communis*** cocoon loses water at approximately double the rate lost by three common aerial species (*Achaeranea tepidariorum*, *Argyrodes trigonum*, and *Uloborus glomosus*). Fritz and Morse (1985) contend that selection of the oviposition site is "one of the most important decisions made" by organisms that deposit eggs externally. Hieber (1985) demonstrated this same importance in the cocoon-carrying ***Argiope aurantia***, where the outer cocoon layer provides the air space that does most of the insulating.

Figure 70. ***Frontinella communis*** (**Linyphiidae**), a spider that deposits her eggs near the soil where water loss is less than at the aerial position of her food web. Here she is on the underside of the web. Photo by William DuPree, with permission.

Figure 71. ***Frontinella communis*** (**Linyphiidae**), the bowl and doily spider, on its web. This species makes a double web, hence its common name. Photo by Robert Klips, with permission.

Hence, we should look at moss-dwelling species for differences in the ability of their cocoons to maintain adequate moisture levels and to prevent excess moisture compared to aerial species. We know that ***Hickmanapis minuta*** (**Anapidae**) will attach its egg sacs to mosses (Hickman 1943). It is likely that a number of others do the same.

Overwintering

Spiders typically live only about two years, so it would not seem expedient for their overwintering strategy to be a strong evolutionary driver. Nevertheless, they must survive at least one winter, and strategies vary. In the **Thomisidae**, there seems to be no special overwintering structure – no web or burrow (Lissner 2011c).

But for some spiders, mosses are essential to winter survival. ***Larinia jeskovi*** (**Araneidae**), living among the sedge *Carex rostrata*, is rare in Europe (Kupryjanowicz 2003). It builds no winter retreat, but females overwinter in areas with a thick, loose layer of mosses. When the moss layer is absent, the abundance of this species is low. In peatlands, ***Sitticus floricola*** (Figure 72-Figure 73; **Salticidae**) overwinters deep in the ***Sphagnum*** (Harvey *et al*. 2002).

Figure 72. ***Sitticus floricola*** (**Salticidae**) among mosses. Photo ©Pierre Oger, with permission.

Figure 73. ***Sitticus floricola*** (**Salticidae**) on web. Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.

Spider Guilds

Root (1967) defined a guild as "a group of species that exploit the same class of environmental resources in a similar way." This uses terminology familiar from the niche concept, but confines members of a guild to a class of resources rather than all of them.

The concept of guild may be useful in describing the spider communities of bryophytes, but such a description has not yet been constructed. Cardoso *et al*. (2011) defined spider guilds in large scale view for the first time. They used foraging strategy (type of web and method of active hunting), prey range (narrow or wide diversity), vertical stratification (ground or vegetation) and circadian activity (diurnal or nocturnal). This resulted in eight guilds, based on feeding strategy: (1) sensing weavers; (2) sheet weavers; (3) space weavers; (4) orb web weavers; (5) specialists; (6) ambush; (7) ground; and (8) other hunters. Using this classification, Cardoso and coworkers found that the correlation of guild richness or abundances was generally higher than the correlation of family richness or abundances. Nevertheless, guilds tended to include related species because among spiders the web-building strategy and form of the feeding apparatus are the basis of higher classification. Therefore, it is not surprising that families serve as good surrogates, forming similar groupings.

If we attempt to describe the predominant spider guilds among bryophytes, it might provide a framework for examining the habitats where they live. Certainly the **ground-hunting guild** is common on the surface of bryophytes in bogs and open habitats such as sand dunes and grasslands or meadows. Cardoso *et al*. (2011) found that **ground hunters** formed the largest guild (number of families) worldwide. The **sheet-weavers** and **other hunters**, including the **Linyphiidae**, are predominant among bryophytes in most habitats. Surprisingly, the **ground hunters** have the largest family representation among the bryophytes, but the number of species is not large, and representation differs with habitat. Each of the guilds is represented by one or more families among the bryophytes:

Sensing web: Atypidae
Sheet web: Amaurobiidae, Dipluridae, Eresidae, Hahniidae, Linyphiidae (Linyphiinae, Micronetinae)

Space web: Dictynidae (Dictyninae), Micropholcommatidae
Orb web: Anapidae, Araneidae, Symphytognathidae
Specialist: Mimetidae
Ground hunters: Corinnidae, Gnaphosidae, Liocranidae, Lycosidae, Zoridae
Other hunters: Clubionidae, Linyphiidae (Erigoninae), Philodromidae, Salticidae
Ambush hunters: Thomisidae

I have omitted the **Cybaeidae** because the one species (***Argyroneta aquatica***) reported herein uses an underwater nest and darts out to catch prey, not catching them with a web as used for the guild classification.

Adaptations to Bryophytes

For spiders, living among bryophytes seems to be mostly an advantage for the spiders, not the bryophytes. The provision of cover and moisture by the bryophyte is complemented by providing avoidance of larger predators. Loss of water would result in loss of hydrostatic pressure in the legs, making it impossible to extend their legs, hence making them unable to escape. The moisture within a moss mat should therefore make mobility easier than in a drier location.

In other groups of animals, color patterns have presented good adaptations. There seems to be little discussion of this as an adaptation for bryophyte-living, and certainly green spiders are rare. However, coloring of spiders is often disruptive, as seen for ***Sitticus floricola*** (Figure 72-Figure 73; **Salticidae**) and the disruptive pattern of the spider in Figure 74.

But to live among bryophytes can be somewhat demanding on the construction of the spider. Bryophytes do not provide an easy landscape for navigation for larger spiders. Within the protective cover, jumping is usually not an option. The higher moisture content could save energy that might be needed to provide a thicker cuticle for spiders living in drier habitats. But being small is an important adaptation, permitting easy navigation and being compensated by the higher moisture levels available. The moss furthermore buffers the rain so that it does not easily dislodge the spider, and spiders are able to move about sufficiently to avoid drowning in areas of water collection such as leaf bases.

Figure 74. This spider blends well as it traverses the moss ***Didymodon cordatus*** in Europe. Photo by Michael Lüth, with permission.

Several families stand out among bryophyte dwellers. The one with the greatest number of bryophyte-dwelling species is the **Linyphiidae**, a family of spiders generally less than 2 mm long. Bryophyte-dwelling spiders are also found within many other spider families, especially including the **Gnaphosidae** (ground spiders), **Clubionidae** (foliage spiders), and **Theridiidae** (comb-footed spiders), some of which are considerably larger. In New Zealand, the **Micropholcommatidae** have a number of bryophyte-dwelling species.

Anapidae

The **Anapidae** are orb weavers, often with webs less than 3 cm. Given the small size (mostly less than 2 mm) and habits (Wikipedia 2010a) of this family, we should look for heretofore unknown species among the bryophytes. Kropf (1997) has shown that one member, *Comaroma simoni* (Figure 75), a member of the **Anapidae**, is born without a hardened covering, a characteristic that likely applies to other species as well. Such species are thus subject to greater desiccation than adults (Kropf 1997), a problem that could be ameliorated by bryophytes. Nonetheless, this species is a soil dweller in Austria and in the scree areas of mountains in Europe, it occurs exclusively in association with bare rock (Růžička & Klimeš 2005). Kropf suggests that in the beech (*Fagus sylvatica*) forests of Austria this species most likely undergoes vertical migration to reach the best moisture and temperature conditions. In many habitats, such behavior could make the bryophyte an important part of a daily and seasonal cycle for some taxa, even if only to increase the soil moisture.

The **Anapidae** live primarily in tropical rainforests of New Zealand, Australia, and Africa, with scattered occurrences on other continents, where bryophytes (and leaf litter) commonly provide them a home on the ground (Wikipedia 2013). ***Pseudanapis aloha*** (**Anapidae**), is known from mosses in the mountains of Hawaii, USA.

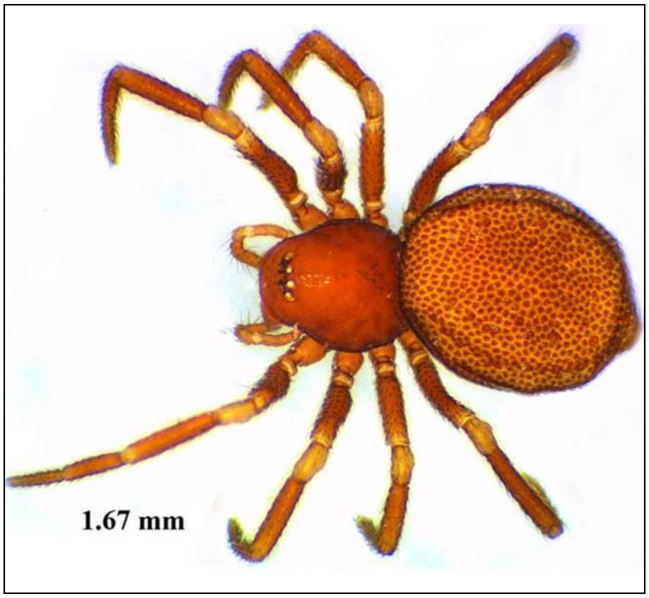

Figure 75. ***Comaroma simoni***. Photo ©Pierre Oger, with permission.

Clubionidae (Sac or Tube Spiders)

These spiders make tubes where they hang out during the day. These tubes are located under stones, loose bark, between moss, and between leaves. At night they are hunters. On Mount Kilimanjaro, Denis (1950) found the 12 mm ***Clubiona abbajensis kibonotensis*** under moss [(see *C. reclusa* (Figure 76-Figure 78) and *C. pallida* (Figure 79)].

Figure 76. ***Clubiona reclusa***, a generic relative of ***Clubiona abbajensis kibonotensis***, in nest with egg sac on a fern frond. Photo by Jørgen Lissner, with permission.

Figure 77. ***Clubiona reclusa*** egg sac from fern frond. Photo by Jørgen Lissner, with permission.

Figure 78. ***Clubiona reclusa*** male. Photo by Jørgen Lissner, with permission.

Figure 79. ***Clubiona pallidula***, a generic relative of ***Clubiona abbajensis kibonotensis*** that lives under mosses on Mount Kilimanjaro. Photo by Trevor and Dilys Pendleton <www.eakringbirds.com>, with permission.

Gnaphosidae (Ground Spiders)

The **Gnaphosidae** (Figure 80) form a worldwide family with over 2000 species (Wikipedia 2012c). They do not construct a web for capturing prey, but instead are night-active hunters. They spend the daylight hours in a silken retreat. The females guard their thick-walled eggs until the spiderlings hatch.

Figure 80. ***Gnaphosa muscorum*** (**Gnaphosidae**) on leaf. Photo by Tom Murray, with permission.

Linyphiidae (Sheet Spiders)

If any family may be considered adapted to living among bryophytes, it is the **Linyphiidae**. This is the largest family of spiders [more than 4,300 described species in 578 genera worldwide (Wikipedia 2012b)], so it is not surprising that its species comprise the majority of bryophyte dwellers. Their tiny size (1-10 mm) makes them difficult to find and identify. Hence, there are likely many more species than those already described.

The shape of the **Linyphiidae** is somewhat different from that in many other spider families. The thorax is reduced relative to the abdomen, and the abdomen is humped or globular, making it the conspicuous part of the spider (Figure 81). Is this an adaptation that permits a relatively large amount of the body to be available for reproduction while making a smaller size possible for the animal overall?

Figure 81. ***Linyphia triangularis*** showing body shape. Photo by James K. Lindsey, with permission.

Linyphiidae build sheet or dome-shaped webs (Figure 82), hence the common names of sheet weavers or sheet spiders, with no retreat, and spend their time hanging upside down on the underside of the sheet (Nieuwenhuys 2010). Flying insects become ensnared by the web and fall to its lowest point where the awaiting spider bites it through the net (Lissner 2011c). In Jutland, Denmark, the female shadow hammock spider, ***Labulla thoracica*** (Figure 83), is known to weave her web under a moss mat (Hormiga & Scharff 2005).

Figure 82. Horizontal webs at Shiretoko Goko, Japan, such as those manufactured by members of the **Linyphiidae**. Photos by Janice Glime.

Figure 83. ***Labulla thoracica***, a spider that weaves webs beneath moss mats. Photo by Ondřej Machač, with permission.

Dispersal in the **Linyphiidae** is often accomplished by **ballooning**, a phenomenon in which the spider ascends to something taller, like a fence, points the spinnerets upward, then secretes a thread (Pratt 1935; Lissner 2011c). It jumps or is blown with the thread serving as an anchor. On a good wind, it can accomplish a greater distance. For these small spiders, this is more than could be accomplished by walking, and the thread provides an anchor so that they don't get too far from their current suitable habitat. It is a lot like bungee jumping, except a lot of their travel is horizontal. These spent bungee cords can actually be noticeable when many spiders balloon in a short period of time, as may occur in late summer. Individuals will also keep trying if they are unsuccessful in travelling very far, contributing to the accumulation of threads on the ground.

Within the **Linyphiidae**, the subfamily **Erigoninae** is a group of small spiders that are mostly less than 3 mm long. In some members of ***Walckenaeria***, including a number of moss dwellers, eyes of males are located on a pedestal or turret (Figure 84-Figure 85), creating a periscope. But this would-be periscope provides little visual contribution. Rather, it serves a sexual function, possibly secreting sexual pheromones (Millidge 1983). There is some evidence that the female grabs it during courtship or mating, as known in the linyphiid ***Hypomma bituberculatum***.

Figure 84. ***Walckenaeria acuminata*** male on a moss, showing the stalk that houses the eyes. Photo by Jørgen Lissner, with permission.

Figure 85. ***Walckenaeria cucullata*** male on moss, providing a front view of the stalk with eyes. Photo by Jørgen Lissner, with permission.

Lycosidae (Wolf Spiders)

Contrasting with these small species, the larger ***Pardosa maisa***, a wolf spider (*cf.* Figure 86), lives in a poor pine fen where there is a "rich" ***Sphagnum*** layer (Itaemies & Jarva 1983). Peatlands and mires have their unique fauna of spiders (Vilbaste 1981). Villepoux (1990) found that ground-level spiders in a French peat bog formed several representative groups, each helping to define a biotope. In fact, he felt that only a few species of spiders were sufficient to estimate the diversity of the plant communities in this habitat. In bog and fen habitats, several members of this family are dominant, running about on the surface rather than within the mat, and no doubt taking advantage of the moist mosses to retain their moisture in the drying rays of the sun. Other sunny habitats for moss inhabitants of this family include the open tundra (Dondale *et al*. 1997), sand dunes (Merkens 2000), and as invaders after fires (Larrivée *et al*. 2005).

Figure 86. ***Pardosa amentata*** female with egg sac, a wolf spider related to the ***Sphagnum*** spider ***P. maisa.*** Photo by James K. Lindsey, through Wikimedia Commons.

Symphytognathidae and Micropholcommatidae

The family includes some very small spiders, some of which are known moss-dwellers. The Samoan moss spider (***Patu marplesi***; **Symphytognathidae**) is often considered to be the world's smallest spider (Alphonse 2010), having a leg span of only 0.5 mm (King 2004). However, in other members of this genus only the female is known. Since the male is typically smaller, it is possible that other species may be smaller, in particular *Patu digua* (Wikipedia 2010c) that is often designated as the smallest. ***Patu marplesi*** is known from mosses in New Zealand (Forster 1959). The family **Micropholcommatidae** is a segregate of **Symphytognathidae** and includes ***Textricella*** a genus with a number of known moss dwellers. ***Textricella nigra*** (**Micropholcommatidae**) is known from moss on tree trunks at 1000 m asl and the type is known from moss, both in New Zealand; ***T. propinqua***, ***T. pusilla***, ***T. salmoni***, ***T. scuta***, ***T. signata***, ***T. tropica***, ***T. vulgaris*** (many records), ***Micropholcomma bryophilum***, ***Parapua punctata***, ***Pua novaezealandiae***, ***Zealanapis australis*** (as ***Chasmocephalon armatum***), all members of **Micropholcommatidae,** occur among mosses in New Zealand. ***Patu woodwardi*** (as *Mismena woodwardi*; **Symphytognathidae**) from New Guinea and ***Textricella hickmani*** and ***T. parva*** from Tasmania are known from mosses.

Theridiidae (Tangle-web Spiders, Cobweb Spiders, and Comb-footed Spiders)

This family (Figure 87) is likewise among the larger families with over 2200 species (Wikipedia 2012d). The females often build a tangle web (3-d) instead of a simpler sheet. Their web construction uses a sticky silk to capture prey instead of the more common woolly silk. Many other theridiids trap ants and other ground-dwelling insects with their elastic sticky silk trap lines that lead to the soil surface. It would be worth searching for these traplines among bryophytes. The family includes the well-known widow spiders. The largest genus is ***Theridion***, which includes some members among mosses (Logunov *et al*. 1998).

Figure 87. ***Robertus pumilus***, member of a genus in which some members inhabit bryophytes. Photo by Tom Murray, through Creative Commons.

Summary

Spiders are in the subphylum **Chelicerata**, Class **Arachnida**, Order **Araneae**. Spiders have eight legs attached ventrally to the **cephalothorax**. Some occur on the surface of moss beds where mosses provide moisture, but others live within moss beds and cushions. Because of their tiny size and habit of living within moss mats or cushions, some, perhaps many, spiders never go near pitfall traps commonly used for collecting. More diversity is likely if one uses a combination of pitfall traps, light traps, soil sifters (sieving), and hand collections. Because of widespread use of only pitfall traps, our knowledge of bryophyte-dwelling spiders most likely underestimates the importance of the bryophyte habitat for diversity. Spiders considered rare are likely to occur among bryophytes, in part due to inadequate sampling, and in other cases due to rarity of a particular habitat.

The growth form of bryophytes may play a role in the choice of habitat, but no study specifically tests this hypothesis, although different spider communities have been found on different growth forms. Small members of **Linyphiidae** have the most moss-dwelling species in most habitats, with **Lycosidae** having more biomass in open habitats of bogs, tundra, dunes, and sites after fire.

Spiders are susceptible to water loss and may use bryophytes as a moist retreat as well as a hideaway from predators. The bryophyte cover also protects them from the heat and UV rays of the sun, with higher temperatures causing a greater water loss. Bryophytes serve as sites for reproduction, nests, and food webs. Some spiders use mosses as a winter refuge. Spiders will locate their nests to optimize temperature, thus optimizing energy gain.

Spiders use claws with fangs to inject venom into their prey. Some use webs to trap and others hunt their prey. Spiders are carnivores and most likely never eat bryophytes. However, bryophytes can serve as a source of food by harboring food organisms, including other spiders, insects (esp Collembola), and earthworms.

The most common spider families to be found associated with bryophytes are Anapidae, Clubionidae (sac or tube spiders), Gnaphosidae (ground spiders), Linyphiidae (sheet spiders), Lycosidae (wolf spiders), Symphotognathidae, Micropholcomatidae, Theridiidae (tangle-web spiders, cobweb spiders, and comb-footed spiders). All eight spider guilds are present among mosses. The adaptations of spiders to living among bryophytes may include disruptive coloration and small size, with maneuverability limiting larger spiders. Bryophytes are the sites for webs of some species and for placing eggs for others. They provide buffered temperature and humidity locations for dormant stages, including overwintering. Some members of the **Linyphiidae**, the most species-rich family among bryophytes, care for their young by providing food, but most young spiderlings are on their own.

Dispersal in large spiders is typically accomplished by running, but in the tiny **Linyphiidae**, ballooning and bungee jumping can help them to get to greater distances than is feasible for their tiny legs.

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