

CHAPTER 7-4

ARTHROPODS: SPIDERS AND PEATLANDS

Janice M. Glime and Jørgen Lissner

TABLE OF CONTENTS

Bogs and Fens	7-4-2
Bryophytic Accommodations.....	7-4-3
Moisture Relationships	7-4-3
Temperature Relationships.....	7-4-6
Spider Mobility	7-4-7
Abundance and Dominance	7-4-7
Tyrphobionts	7-4-10
Specialists and Rare Species	7-4-12
Mosses as Spider Habitats in Bogs and Fens	7-4-16
Is <i>Sphagnum</i> Special?	7-4-16
The Bog and Fen Habitat	7-4-19
Hummocks and Hollows.....	7-4-19
Indirect Association with <i>Sphagnum</i>	7-4-19
Differences among Bogs and Fens.....	7-4-21
Niche Separation – Lycosidae.....	7-4-21
Bryophytes and Trap-door Spiders	7-4-23
Bryophytes Hide New Species.....	7-4-23
Conservation Issues.....	7-4-24
Peatland Fire Communities	7-4-25
Summary	7-4-29
Acknowledgments.....	7-4-30
Literature Cited	7-4-30

CHAPTER 7-4

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Figure 1. A spider's view of *Sphagnum capillifolium*. Photo by Michael Lüth, with permission.

A number of studies have investigated the spider fauna of peat bogs, *e.g.* Villepoux (1990), Kupryjanowicz *et al.* (1998), Koponen (2000), and Scott *et al.* (2006). Some studies have been aimed at ecological aspects such as investigating the spider fauna assemblages of different bog types, others have been aimed at comparing assemblages as a function of shading or assessing spider indicator species of conservation value. Rėlys and Dapkus (2002) demonstrated the high degree of dissimilarity between spiders in pine forests and bogs in southern Lithuania. Few studies dealing directly with spiders and preferred moss species are known to us. Most information is scattered in the literature, and in most instances only relate spider habitats in respect to mosses to higher taxonomical levels such as "among moss" or "in *Sphagnum* bogs" (Figure 1).

Bogs and Fens

The nomenclature used for labelling the various types of bogs and fens has been inconsistent among the continents and even within continents, especially when considered over time. This makes it somewhat difficult to make adequate comparisons between studies when one is not familiar with the specific location. The fact that current

usage is based on water and nutrient source to define these habitats into **bog** (raised bog with only precipitation as water and nutrient input), vs **fen** (nutrients and water sources include ground water) makes it even more difficult to determine the category based on published studies alone. The fen is further divided into **poor**, **intermediate**, and **rich fen**, again based on nutrient levels. These distinctions may influence the spider fauna, but as will be documented in some of the studies below, the flora (usually described by the tracheophytes) may be the more important character for describing the spider habitat.

Many studies have catalogued the spiders in peatlands around the world, but especially in Europe. This even broader term of peatlands can include grasses and sedges with no or few mosses and lacking *Sphagnum* completely. Although authors often did not distinguish the substrate used by the spiders, it is reasonable to surmise that the spiders' presence was because the mosses that dominate the ground surface of the bog or fen provided the conditions needed for their lives (Figure 1), even if that is to provide a habitat suitable for shrubs and trees that the spiders inhabit. *Sphagnum* (Figure 2), especially, plays a large role in creating those conditions.



Figure 2. *Sphagnum subsecundum* showing spider webs. Photo by Michael Lüth, with permission.

Bryophytic Accommodations

Humans need to explain things, being curious and asking why. So we ask here why spiders associate with peatlands and their mosses. An obvious consideration is moisture, but the mosses also provide an escape from the sun (heat and light), a location for food, and a refuge from predation. These are the same characteristics typical of bryophyte interactions for most invertebrates. We will examine just how important they are for spiders in the bog and fen habitats.

Moisture Relationships

Moore and Bellamy (1974) discuss maintaining moisture as being among the adaptations of arachnids in "mire" habitats. Mires, bogs, and the various types of *Sphagnum* (Figure 1) peatlands have an increasing temperature upward and an increasing humidity downward. Nørgaard (1951) presented this gradient for a Danish *Sphagnum* bog (Table 1). Kajak *et al.* (2000) found that moss and litter layers were important for spiders in both natural and drained fens, with mosses causing the soil under them in the sedge-moss community to have the highest water-holding capacity and the greatest moisture stability throughout the year.

Table 1. Gradation of temperature and humidity in a Danish *Sphagnum* bog. From Nørgaard 1951.

	Diurnal Temperature Fluctuation	Relative Humidity
100 cm above surface	26°C	<40%
At mire surface	33°C	<40%
100 cm below surface	5°C	100%

A particularly helpful study is one by Biström and Pajunen (1989) examining the arachnid fauna occurring in association with *Polytrichum commune* (Figure 3), *Sphagnum girgensohnii* (Figure 4), and *S. squarrosum* (Figure 5) during May – October 1988 at two locations in southern Finland. All three of these mosses can occur in light shade with high water content. The life forms of these three mosses differ, with the sun-loving *P. commune* being

slender and upright, forming tall turfs, and sometimes having limited space between the stems, especially for larger spiders; it furthermore has a waxy leaf surface that does less to maintain surface moisture. *Sphagnum girgensohnii* is more shade-loving and provides relatively open spaces among the stems while creating a much greater canopy to intercept light and protect from UV radiation than one would expect from within the *P. commune* turf. *Sphagnum squarrosum* has a similar life form to that of *S. girgensohnii*, but it has larger leaves and a more succulent appearance.



Figure 3. *Polytrichum commune*, illustrating the waxy appearance of the leaves that hold little water compared to *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 4. *Sphagnum girgensohnii*, a treed fen species that provides habitat for spiders. Photos by Janice Glime.



Figure 5. *Sphagnum squarrosum*, a woodland species that harbors spiders. Photo by Janice Glime.

When Biström and Pajunen sieved the mosses they retrieved 1671 arthropod specimens. Among these were 1368 Araneae represented by 77 species, 35 Pseudoscorpionida represented by 1 species, and 157 Opiliones represented by 5 species. Other arthropods included Diplopoda (39/4), Chilopoda (43/3), and Symphyla (9/1). Mites (Acarina) were not included in the study. Our climate in the Keweenaw Peninsula, Michigan, USA, is similar to the climate of Finland, but I (Glime) must confess that I have never found pseudoscorpions or harvestmen among any moss collections. Perhaps I simply was not observant at the right times.

Biström and Pajunen identified three moisture content levels (dry, moist, and wet) among these Finnish mosses and estimated the number of individuals per sample in each of these three conditions. They then estimated the number of individuals of each major spider species per sieved sample in each category (Table 2). Species that tended to occur in drier stands included the **Linyphiidae** *Dicymbium tibiale* and *Tenuiphantes alacris*. Those that seemed to prefer moister mosses included the **Linyphiidae** *Centromerus arcanus*, *Minyriolus pusillus*, and *Tapinocyba pallens*. They found that the spider *Walckenaeria kochi* (Figure 61; **Linyphiidae**) occurred only on *Polytrichum commune*, suggesting a preference for a drier habitat than that afforded by the five *Sphagnum* species present. Palmgren (1975) considered the optimum habitat for *Centromerus arcanus* to be moist spruce forest with a *Sphagnum* (Figure 1) carpet. The only spider community that seemed to differ significantly was that of *Sphagnum girgensohnii*, a grouping that was revealed by cluster analysis.

In addition to the moisture contained within the *Sphagnum* (Figure 1) mat, peatlands can give spiders a convenient access to open water, particularly for amphibious and "aquatic" species. Amphibious spiders that live in bogs are able to run along the surface of the water (Figure 6) until they reach a plant (Figure 7) (Nørgaard 1951). They can then climb down the plant, using the leverage gained from the plant attachment to break through the surface tension and climb down into the water.

Table 2. Abundance (individuals per sample) of widespread spider taxa in each of three moisture categories in Finnish forested boggy areas. From Biström & Pajunen 1989.

	dry	moist	wet
<i>Dicymbium tibiale</i>	0.87	0.39	0.24
<i>Semljicola faustus</i>	0.10	0.14	0.28
<i>Minyriolus pusillus</i>	0.03	0.10	0.23
<i>Tapinocyba pallens</i>	0.05	0.09	0.13
<i>Walckenaeria cuspidata</i>	-	0.04	0.04
<i>Centromerus arcanus</i>	0.82	0.95	1.45
<i>Tenuiphantes alacris</i>	0.48	0.28	0.11
<i>Macargus rufus</i>	0.13	0.12	0.06
<i>Neon reticulatus</i>	0.02	0.04	0.06
<i>Robertus scoticus</i>	0.03	0.18	0.09



Figure 6. *Pirata piraticus* walking on the water surface. Photo by Trevor and Dilys Pendleton at <<http://www.eakringbirds.com/>>, with permission.



Figure 7. *Pirata piraticus* climbing on a plant at the water surface. Photo by Michael Hohner, with permission.

But spiders in bogs are not just about water. Rather, this specialized fauna reflects not only the microclimate

and physical factors, but also the lack of disturbance, the age of the habitat, and the surrounding vegetation that may supply new fauna or serve as a refuge during certain times of the year (Bruun & Toft 2004). For the small spiders like the **Linyphiidae**, where long distance travel is difficult, stability is key. And ability to maintain body moisture is part of that.

Regular flooding effectively prevents some species from inhabiting various wetlands. In particular, Bruun and Toft (2004) found that the **Linyphiidae** were absent at Gjesing Mose, Denmark, attributing the absence to frequent flooding. On the other hand, they were present in other locations where the moss was floating, hence avoiding flooding of the spider habitat. Under moderate fluctuations in water level, some spiders are able to retreat upward into the hummocks. Other spiders such as *Maro lepidus* (Figure 38; **Linyphiidae**) take advantage of the water, preferring hollows over hummocks (Koponen 2004). This species was also found by Komposch (2000) in wetlands of Austria.

Kupryjanowicz *et al.* (1998) found a large proportion of **hygrophilous** (water-loving) species in the raised peat bogs of Poland. Humidity and illumination were the major determinants of the spider fauna. In the sunlit areas of the bog, two wolf spiders (**Lycosidae**), *Pardosa sphagnicola* (Figure 8) and *Arctosa alpigena lamperti* (Figure 51) dominated the spider fauna. Since these are larger spiders, it is likely that they are more tolerant of the drying sun because of their lower surface area to volume ratio. Their dominance in peatlands is a shift from the dominance of **Linyphiidae** among mosses in most drier habitats. The somewhat loose arrangement of the *Sphagnum* (Figure 1) branches below the surface might permit them to retreat there when they need to replenish moisture, avoid UV light, or escape from predators.



Figure 8. *Pardosa sphagnicola* female on *Sphagnum*. Photo by Walter Pfliegler, with permission.

The moisture relations of spiders in bogs are reflected in the ability of the bogs to support species that are also common in marshes and other wetlands. For example, in Poland Kupryjanowicz (2003) found some of the most common **sphagnophilous** species, including **Hahniidae**: *Antistea elegans* (Figure 9), **Lycosidae**: *Pardosa sphagnicola* (Figure 8), *Pirata tenuitarsis* (Figure 10), and *P. uliginosus* (Figure 33) in the sedge-moss marshes.

Other peat bog species present in these marshes were the **Gnaphosidae**: *Drassyllus lutetianus* (Figure 11) and *Gnaphosa nigerrima* (Figure 12) – a species mostly restricted to *Sphagnum* carpets of moors in Germany (Platen 2004), and **Salticidae**: *Neon valentulus* (Figure 13). The **Linyphiidae** were also present, represented by *Aphileta misera* (Figure 36), but this family is much more species-rich elsewhere.



Figure 9. *Antistea elegans* (**Hahniidae**). Photo by Jørgen Lissner, with permission.



Figure 10. *Pirata tenuitarsis* (**Lycosidae**) male among *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 11. *Drassyllus lutetianus* (**Gnaphosidae**). Photo by Jan Barvinek, through Creative Commons.



Figure 12. *Gnaphosa nigerrima* (Gnaphosidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 14. *Walckenaeria furcillata* (Linyphiidae). Photo by Jørgen Lissner, with permission.



Figure 13. *Neon valentulus* (Salticidae), a known peat bog species. Photo by Sarefo, through Wikimedia Commons.



Figure 15. *Synageles hilarulus* (Salticidae) among bryophyte and needle litter. Photo by Stefan, Schmidt through Creative Commons.



Figure 16. *Trochosa robusta* (Lycosidae) female, a species that lives in bogs but is adapted to dry habitats. Photo by Jørgen Lissner, with permission.

On the other hand, it appears that many of the spiders in bogs are actually **xerophiles** (dry-loving), permitting them to survive the dry heat of summer in exposed areas of the bog. For example, *Walckenaeria furcillata* (Figure 14; **Linyphiidae**) is a widespread species that occurs not only under heather and scrub, and among mosses and grasses on acid heathland, but also occurs in deciduous woodlands, calcareous grassland, and fens (Dawson *et al.* in prep). *Synageles hilarulus* (Figure 15; **Salticidae**) is a sub-boreal species (Logunov 1996) that runs about in search of food, but in the Mediterranean region, it occurs in grassland (Telfer *et al.* 2003). *Trochosa robusta* (Figure 16; **Lycosidae**) lives predominately on dry grassland of limestone, but can also be found on the oligotrophic moors (Platen 2004). These spiders can escape excessive moisture by climbing plants or hummocks.

Temperature Relationships

Although it is sometimes difficult to separate the effects of temperature from those of moisture, certainly the *Sphagnum* (Figure 1) mat provides a gradient of both, as seen in Table 1. The surface experiences greater extremes of both (Figure 87), making the mat a suitable refuge for some spider species. The differences between surface

conditions and those within the peat layer can provide adequate niche separations in a short vertical distance. Nørgaard (1951) cites the vertical separation of two members of **Lycosidae**, *Pirata piraticus* (Figure 17) and *Pardosa pullata* (as *Lycosa pullata*; Figure 18-Figure 19), in a Danish *Sphagnum* (Figure 1) bog in relation to temperature and humidity. *Pirata piraticus* lives among the *Sphagnum* stalks (Figure 4) where the relative humidity remains a constant 100% and the temperature varies only about 5°C within a day. At the surface (Figure 1), however, where *Pardosa pullata* lives, the humidity varies between 40 and 100% on a single day with temperature variations up to 30°C within a day. *Pardosa pullata* is physiologically adapted to this fluctuation, with a higher temperature preference and a higher thermal death point than those of *Pirata piraticus*. The latter species also has a greater sensitivity to low humidities. This relationship is described in greater detail later in this subchapter.



Figure 17. *Pirata piraticus* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.



Figure 18. *Pardosa pullata* (**Lycosidae**) male on mosses. Photo by Jørgen Lissner, with permission.



Figure 19. *Pardosa pullata* (**Lycosidae**) female with egg sac on *Sphagnum*. Photo by Jørgen Lissner, with permission.

Spider Mobility

Perhaps one limiting factor for spiders among bog and fen bryophytes is the problem of mobility. First, they must arrive, so that for restored peatlands, this can be a serious detriment to species diversity and the specialists are likely to be the last to arrive because they must traverse unfriendly territory to get there. Some spiders are highly mobile compared to others. The larger spiders like **Lycosidae** (wolf spiders) are able to run across the surface, and as most of us have witnessed, these can run fairly quickly and traverse considerable distances compared to such spiders as the tiny **Linyphiidae**. Hence, the larger spiders, especially the **Lycosidae**, are more common on peatlands, especially during restoration, than in other bryological habitats. *Gnaphosa nigerrima* [6.7-9.1 mm (Grimm 1985); Figure 12; **Gnaphosidae**] is widespread in northern Europe and Asia, where it is common on *Sphagnum* lawns (Figure 1). Its presence in pitfall traps among *Sphagnum* (Harvey *et al.* 2002) reflects its ability to run about swiftly at night. Nevertheless, it is unable to cross a fragmented landscape to recolonize restored wetlands. This is evident in Denmark, where it only occurs in the very best (undisturbed) bogs. This species demonstrates the importance of broad ecological amplitude in enabling spider dispersal.

Abundance and Dominance

Peatlands seem to have a better commonality of dominant species over widespread geographic areas than some of the other communities. This is especially true for the **Lycosidae**, where the genera *Arctosa*, *Pirata*, *Pardosa*, and *Trochosa* are common and often the most abundant, but species vary geographically. Nevertheless, as large spiders, they can be less abundant in numbers than small spiders like the **Linyphiidae**. Biomass comparisons might tell a different story.

Komposch (2000) used a variety of sampling methods (pitfall traps, light-traps, soil-sifter, hand-collecting) to study the spiders in wetlands at Hörfeld-Moor, Austria. This study assessed the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. Surprisingly, the bog had the smallest percentage of red data species (17% endangered) among the habitats sampled. Komposch suggested that the small number of endangered

species in the raised bog may relate to the small size of this habitat in the study area. Fourteen species occurred only in the bog, but were not necessarily bryophyte inhabitants and were often represented by only one or two individuals. The dominant species were members of the **Lycosidae**: *Trochosa terricola* (Figure 20-Figure 21) (30%), *Trochosa spinipalpis* (Figure 22) (22%), and *Pirata hygrophilus* (Figure 23) (10%), all reported elsewhere in this chapter as important species in bogs or fens. *Gnaphosa nigerrima* (Figure 12; **Gnaphosidae**), likewise reported elsewhere in this subchapter, occurred on hummocks (Komposch 2000) in an area where peat was formerly harvested (Rupp 1999).



Figure 20. *Trochosa terricola* female (**Lycosidae**). Photo by Jørgen Lissner, with permission.



Figure 21. *Trochosa terricola* (**Lycosidae**) male on moss. Photo by Jørgen Lissner, with permission.

Kupryjanowicz *et al.* (1998) reported 203 species of spiders in the raised peat bogs of Poland, where *Sphagnum magellanicum* (Figure 24) and *S. rubellum* (Figure 25) dominate the moss layer. The *Sphagnum magellanicum* habitat was dominated by **Lycosidae**: *Pardosa sphagnicola* (Figure 8) (14, 32, and 34% of spiders at three sites) and in the *Vaccinium uliginosum* pinetum, *Pirata uliginosus* (Figure 33) with 19 and 24% at two sites and 39% at another site. *Pardosa sphagnicola* comprised 18% at the latter site. But even rare species were relatively numerous here and in other bogs, especially on more sunlit peat bogs: *Arctosa alpigena lamperti* (Figure 51; **Lycosidae**) (7% in one site), *Gnaphosa microps* (Figure

26; **Gnaphosidae**) (3% in one site), *Pardosa hyperborea* (Figure 52) (3% in one site), *P. maisa* (8% in one site), and *Scotina palliardi* (**Liocranidae**) (3%, 0.03%, 4% in three sites) – a species new to Poland.



Figure 22. *Trochosa spinipalpis* (**Lycosidae**) among *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 23. *Pirata hygrophilus* (**Lycosidae**). Photo by Kjetil Fjellheim, through Creative Commons.



Figure 24. *Sphagnum magellanicum*. Photo by Michael Lüth, with permission.



Figure 25. *Sphagnum rubellum*. Photo by Michael Lüth, with permission.



Figure 26. *Gnaphosa microps* (Gnaphosidae). Photo by Glenn Halvor Morka, with permission.

In bogs of Geitaknottane Nature Reserve, western Norway, the **Lycosidae** again dominated. *Pirata hygrophilus* (Figure 23) showed the highest activity abundance (49.2%), followed by *Pardosa pullata* (Figure 18-Figure 19) (17.2%); *Notioscopus sarcinatus* (Figure 27; **Linyphiidae**) (3.9%), *Pardosa amentata* (Figure 28) (3.3%), and *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**) (3.3%) were also among the most abundant (Pommeresche 2002). However, activity can be misleading, with the distance travelled by the tiny **Linyphiidae** being quite short and often confined to the mosses, keeping them out of pitfall traps.



Figure 27. *Notioscopus sarcinatus* (**Linyphiidae**) on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 28. *Pardosa amentata* (**Lycosidae**). Photo by Jørgen Lissner, with permission.

Biström and Pajunen (1989), in their study of two Finnish peatlands, found 23 species with densities of 1 or more individuals per square meter. They found that in the forested boggy areas they studied, the spider fauna was represented by a few very abundant species and many rarely sampled species. Seven species comprised 66% of the total number of spiders. *Centromerus arcanus* (**Linyphiidae**) was the most abundant spider, with 8.7-24.4 individuals per square meter, and tended to be more frequent in *Sphagnum girgenoshnii*. Other **Linyphiidae** included *Dicymbium tibiale* (1.8-11.9) and *Lepthyphantes alacris* (0.7-8.6). Larger spiders such as *Pirata uliginosus* (Figure 33; **Linyphiidae**) are somewhat less dense (1.4), but more easily seen. *Theonoe minutissima* (Figure 29; **Theridiidae**) is small like a linyphiid but was not as abundant (1.1).



Figure 29. *Theonoe minutissima* (**Theridiidae**) female on moss. Photo by Jørgen Lissner, with permission.

Koponen (2002) compared the spider fauna of Sweden, Finland, and northern Norway. He found that spider communities of the southern sites (hemiboreal) differed from the boreal sites of coniferous taiga and those north of the taiga. In the hemiboreal zone, the **Lycosidae** were dominant, led by *Pirata uliginosus* (Figure 33), along with *Pardosa pullata* (Figure 18-Figure 19), whereas the **Lycosidae** *Pardosa sphagnicola* (Figure 8) and *P. hyperborea* (Figure 52) were dominant in the boreal zones. *Hilaira nubigena* (Figure 30; **Linyphiidae**) and *Pardosa atrata* were dominant north of the taiga. No one species

dominated throughout the study area. In Finland, near the northern limit of the hemiboreal zone, the 20 most abundant species were nine **Lycosidae**, nine **Linyphiidae**, one **Hahniidae**, and one **Philodromidae**. The three boreal zones all had *Pardosa sphagnicola* and *P. hyperborea*, both **Lycosidae**, as their two most abundant species. *Arctosa alpigena* (Figure 51; **Lycosidae**) (as *Tricca alpigena*) was also typical there. In the two northernmost zones [palsa (low, often oval, frost heaves occurring in polar and subpolar climates, containing permanently frozen ice lenses) and coastal hemiarctic bogs], *Hilaira nubigena* (Figure 30; **Linyphiidae**) and *Pardosa atrata* were also common.

In a similar study Koponen (1994) found 169 species of spiders in 14 families in the peatlands of Quebec, Canada. Of these, 73 species occurred only in the temperate-boreal region, 58 only in the subarctic-arctic region, and 38 in both regions. The **Linyphiidae** were the most species-rich family (58.3% of species), an interesting observation in a study using pitfall traps. This family was typical of the subarctic region, with the **Erigoninae** being especially important there. The linyphiid *Ceratinella brunnea* occurred in six of the seven study areas. Typical of peatlands, the **Lycosidae** comprised 12.4% of the species, with *Alopecosa aculeata* (Figure 94) and *Pardosa hyperborea* occurring in six of the seven study areas; **Gnaphosidae** comprised 7.1%. The **Hahniidae**, **Dictynidae**, **Salticidae**, **Liocranidae**, and **Theridiidae** were mostly confined to the temperate and to a lesser extent to boreal regions, although *Theonoe stridula* (**Theridiidae**) occurred in six of the seven study areas. Quebec and southern Ontario bogs had 64% of their species in common in the temperate region, whereas only 27% were in common in the subarctic region. The species from bogs in the Manitoba taiga and Quebec were intermediate with 50% of the species in both. About one-third of the spiders in the Quebec bog are Holarctic.



Figure 30. *Hilaira nubigena* (**Linyphiidae**). Photo by Glenn Halvor Morka, with permission.

In Russia, open *Sphagnum* bogs and bog moss pine forests supported 97 species of spiders (Oliger 2004). The most abundant of these was *Pardosa sphagnicola* (Figure 8; **Lycosidae**). The most common families in pitfall traps were **Lycosidae**, **Gnaphosidae**, and **Liocranidae**, whereas the **Linyphiidae** was represented by the most species. It is

possible that the **Linyphiidae** were more abundant than indicated by the pitfall traps. Members of this family of tiny spiders are likely to spend little time venturing outside their moss habitat.

As in most of the other habitats discussed in Chapter 7-2, the linyphiid genus *Walckenaeria* plays an important role in species diversity. This subchapter likewise includes a number of species of *Walckenaeria* from bogs and fens. In addition to these, Millidge (1983) reported several from "boggy areas" in North America and Greenland, including *W. clavicornis* (Figure 63), *W. redneri*, *W. castanea* (Figure 31), and *W. prominens*. Among these, only *W. castanea* was identified as being in a *Sphagnum* bog.



Figure 31. *Walckenaeria castanea* (**Linyphiidae**). Photo by Tom Murray, through Creative Commons.

Tyrphobionts

Peus (1928) coined the term **tyrphobiont** to define those species that are confined to living in peat bogs and mires. Following this definition, Casemir (1976) listed eight species of spiders as true tyrphobionts in Europe: *Heliophanus dampfi* (Figure 32; **Salticidae**), *Pirata uliginosus* (Figure 33; **Lycosidae**), *Clubiona norvegica* (Figure 34; **Clubionidae**), *Theonoe minutissima* (Figure 35; **Theridiidae**) – a species listed as rare in Slovakia. Representing the **Linyphiidae**, he found *Aphileta* (as *Hillhousia*) *misera* (Figure 36), *Drepanotylus uncutus* (Figure 37), *Hilaira excisa*, and *Maro lepidus* (Figure 38).



Figure 32. *Heliophanus dampfi* (**Salticidae**) on a leaf. Photo by Jørgen Lissner, with permission.

Table 3. The most abundant spider species (>10 individuals), and other interesting bog spider species from Karevansuo bog, Finland. Total number of individuals = 3670; total number of species = 98. From Koponen 2002.

	Indivs.	%		Indivs.	%
<i>Pirata uliginosus</i> (Lycosidae)	885	24.1	<i>Agroeca proxima</i> (Liocranidae)	19	0.5
<i>Pardosa hyperborea</i> (Lycosidae)	802	21.9	<i>Tenuiphantes menegi</i> (Linyphiidae)	18	0.5
<i>Arctosa alpigena</i> (Lycosidae)	159	4.3	<i>Haplodrassus signifer</i> (Gnaphosidae)	17	0.5
<i>Trochosa spinipalpis</i> (Lycosidae)	116	3.2	<i>Scotina pallardi</i> (Liocranidae)	15	0.4
<i>Agyreta cauta</i> (Linyphiidae)	112	3.1	<i>Zelotes latreillei</i> (Gnaphosidae)	15	0.4
<i>Walckenaeria antica</i> (Linyphiidae)	110	3.0	<i>Agroeca brunnea</i> (Liocranidae)	13	0.4
<i>Pardosa sphagnicola</i> (Lycosidae)	99	2.7	<i>Walckenaeria nudipalpis</i> (Linyphiidae)	13	0.4
<i>Alopecosa pulverulenta</i> (Lycosidae)	93	2.5	<i>Lasaeola prona</i> (Theridiidae)	12	0.3
<i>Macrargus carpenteri</i> (Linyphiidae)	5	2.3	<i>Bathyphantes parvulus</i> (Linyphiidae)	11	0.3
<i>Oryphantes angulatus</i> (Linyphiidae)	0	2.2	<i>Centromerus arcanus</i> (Linyphiidae)	11	0.3
<i>Antistea elegans</i> (Hahniidae)	5	1.5	<i>Xysticus lineatus</i> (Thomisidae)	7	
<i>Maro lepidus</i> (Linyphiidae)	5	1.5	<i>Neon valentulus</i> (Salticidae)	6	
<i>Drepanotylus uncatus</i> (Linyphiidae)	49	1.3	<i>Minicia marginella</i> (Linyphiidae)	6	
<i>Pirata piscatorius</i> (Lycosidae)	47	1.3	<i>Zora parallela</i> (Zoridae)	5	
<i>Centromerita concinna</i> (Linyphiidae)	46	1.3	<i>Haplodrassus moderatus</i> (Gnaphosidae)	5	
<i>Pardosa pullata</i> (Lycosidae)	42	1.1	<i>Drassyllus pusillus</i> (Gnaphosidae)	4	
<i>Pirata insularis</i> (Lycosidae)	38	1.0	<i>Pelecopsis parallela</i> (Linyphiidae)	3	
<i>Thanatus formicinus</i> (Philodromidae)	34	0.9	<i>Taranucnus setosus</i> (Linyphiidae)	3	
<i>Meioneta affinis</i> (Linyphiidae)	34	0.9	<i>Pirata piraticus</i> (Lycosidae)	2	
<i>Bathyphantes gracilis</i> (Linyphiidae)	33	0.9	<i>Theonoe minutissima</i> (Theridiidae)	2	
<i>Stemonyphantes lineatus</i> (Linyphiidae)	33	0.9	<i>Gnaphosa microps</i> (Gnaphosidae)	1	
<i>Gnaphosa lapponum</i> (Gnaphosidae)	30	0.8	<i>Maro sublestus</i> (Linyphiidae)	1	
<i>Drassodes pubescens</i> (Gnaphosidae)	26	0.7	<i>Maro minutus</i> (Linyphiidae)	1	
<i>Robertus arundineti</i> (Theridiidae)	21	0.6	<i>Centromerus levitarsis</i> (Linyphiidae)	1	
<i>Tallusia experta</i> (Linyphiidae)	20	0.5	<i>Meioneta mossica</i> (Linyphiidae)	1	
<i>Bolyphantes luteolus</i> (Linyphiidae)	20	0.5	<i>Walckenaeria capito</i> (Linyphiidae)	1	



Figure 33. *Pirata uliginosus* (Lycosidae) male subadult among *Sphagnum*. Photo by Walter Pfliegler, with permission.



Figure 34. *Clubiona norvegica* (Clubionidae) on mosses. Photo by Walter Pfliegler, with permission.



Figure 35. *Theonoe minutissima* (Theridiidae) on *Sphagnum*. The female of this small comb-footed spider, measures just 1.2 mm. Photo by Rudolf Macek, with permission.



Figure 36. *Aphileta misera* (Linyphiidae) on *Sphagnum*. Females are 2 mm. Photo by Morten D. D. Hansen, with permission.



Figure 37. *Drepanotylus uncatus* (Linyphiidae), another widespread Palearctic moss inhabitant, where it occurs in bogs and more rarely in neutral or alkaline mesotrophic fens. Photo by Rudolf Macek, with permission.



Figure 38. *Maro lepidus* (Linyphiidae) female on moss. Photo by Jørgen Lissner, with permission.

Are these tyrphobiont designations supported by other studies? We find that the suitability of the designation can vary by country. It is interesting that Casemir (1976) considered *Drepanotylus uncatus* (Figure 37; Linyphiidae) and *Maro lepidus* (Figure 38; Linyphiidae) to be tyrphobionts, whereas at Hörfeld-Moor in Austria, these species were present in some habitats, but not in the bog (Komposch 2000). And even in Great Britain, *Clubiona norvegica* (Figure 34; Clubionidae) occurs in wet places of the high moorland in other mosses as well as

Sphagnum (Harvey *et al.* 2002). *Hilaira excisa* (Linyphiidae) is even more puzzling, for we were unable to find any other record of this species from *Sphagnum* bogs, although our search was definitely not comprehensive. In Denmark it occurs in mossy springs with seeping cold groundwater (cold in the summer). Furthermore, in the Tyne Valley, UK, *Hilaira excisa* lives among grass, rushes, and moss in swamps (Jackson 1906).

Neet (1996) hypothesized that the tyrphobionts should serve as indicators of "good-state" peat bogs. However, the analysis was confounded by the strong relationship between peat bog area and number of tyrphobiont species (Kendall's rank correlation $\tau = 0.65$). Neet (1996) showed that the number of tyrphobiont species of seven European peat-bogs increased as the area of the bog increased. He pointed out that in addition to the species-area relationship, insufficient sampling effort, biogeographical effects and isolation, and perturbations causing local extinctions all contribute to absent tyrphobionts. As in the analysis above, Neet (1996) pointed out that later evidence does not support all members of Casemir's (1976) list as tyrphobionts. He found that under conditions where the preferred peatland habitat is scarce, some of these tyrphobionts could occur in other habitats, including *Pirata uliginosus* (Figure 33; Lycosidae) and *Drepanotylus uncatus* (Figure 37; Linyphiidae) (Hänggi 1987; Hänggi *et al.* 1995). I (Lissner) likewise found *Drepanotylus uncatus* in non-peatland habitats in Denmark, but less reliably, among mosses of neutral or alkaline mesotrophic fens. Hence, these are not strict tyrphobionts.

Specialists and Rare Species

Bogs are often the home of rare species, and their rarity increases as more bogs get destroyed. One such example of rarity is *Heliophanus dampfi* (Figure 32; Salticidae). *Heliophanus dampfi* is a rare jumping spider, known in the United Kingdom only from Flanders Moss (Stewart 2001) and two other mires, one each in Wales and Scotland (Harvey *et al.* 2002). Nevertheless, it is known as a bog inhabitant in studies elsewhere [Casemir 1976 (Germany); Kupryjanowicz *et al.* 1998 (Poland)].

In a study of the *Sphagnum* (Figure 1) habitats of northwest Russia, Oliger (2004) reported that *Antistea elegans* (Figure 9; Hahniidae), *Arctosa alpigena* (Figure 51; Lycosidae) (as *Tricca alpigena*), and *Gnaphosa nigerrima* (Figure 12; Gnaphosidae), all species reported for bogs elsewhere in this subchapter, were numerous in bogs but rare in forests. Biström and Pajunen (1989) considered that the hahniid *Antistea elegans* (Figure 9) might be a bog specialist, with 1.4 individuals per square meter in one site in Finland, but Kupryjanowicz (2003) has reported it from marshes in Poland.

In England, the rare *Maro lepidus* (Figure 38; Linyphiidae) is only known from acid mires, generally with abundant *Sphagnum* (Boyce 2004). *Erigone psychrophila* (Figure 39; Linyphiidae), *E. dentigera* (as *E. capra*), and *Semljicola faustus* (as *Latithorax faustus*) (Figure 40; Linyphiidae) similarly are bog specialists in upland blanket mires in England, living in saturated *Sphagnum* at the margins of pools. But *Semljicola faustus* is known from mosses among heather in the Faroe Islands (Bengtson & Hauge 1979; Holm 1980) and from peat bogs

as well as among stony debris in North Bohemia (Růžicka & Hajer 1996). *Glyphesis cottonae* (Figure 41; Linyphiidae) and *Centromerus levitarsis* (Figure 42; Linyphiidae) are specialists among *Sphagnum* in acid mires; Dawson *et al.* (in prep.) report *C. levitarsis* from *Sphagnum* in damp woodlands and moors in Great Britain.



Figure 39. *Erigone psychrophila* (Linyphiidae) female on bryophytes. This species prefers saturated *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 40. *Semljicola faustus* (Linyphiidae) female. Photo by Jørgen Lissner, with permission.



Figure 41. *Glyphesis cottonae* (Linyphiidae) on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 42. *Centromerus levitarsis*. Photo by Jørgen Lissner, with permission.

Later Boyce (2011) explored the invertebrate fauna of Dartmoor, UK, bogs. He considered *Walckenaeria nodosa* (Figure 43) to be frequent in bogs and wet heaths. And like others, he found the Linyphiidae to be well represented. He considered the linyphiid *Aphileta misera* (Figure 36) to be a specialist in acid mires. *Bolyphantes luteolus* (Figure 44) is likewise an obligate acid mire associate, occurring in litter and mosses of blanket bogs. It is "scarce" in the UK. *Meioneta mossica* (Figure 45) occurs exclusively on *Sphagnum* (Figure 1) lawns where adults build small webs among upper parts of moss cushions. This species requires abundant bog mosses to make suitable homes. *Araeoncus crassiceps* (Figure 46), *Drepanotylus uncatus* (Figure 37), and *Pirata uliginosus* (Figure 33) live in litter and moss in blanket bogs.



Figure 43. *Walckenaeria nodosa*, a species of bogs and wet heaths. Photo by Rudolf Macek, with permission.



Figure 44. *Bolyphantes luteolus*, an obligate acid mire associate Rudolf Macek, with permission.



Figure 45. *Meioneta mossica*, a species restricted to *Sphagnum* lawns. Photo by Eveline Merche, through Creative Commons.



Figure 46. *Araeoncus crassiceps*, a species that lives among litter and mosses in blanket bogs. Photo by Jørgen Lissner, with permission.

Erigone welchi (Figure 47; **Linyphiidae**) lives in saturated *Sphagnum*, making its webs in the moss cushions just above the water surface (Boyce 2004). *Meioneta mossica* (**Linyphiidae**) builds small webs among the upper layers of the moss cushions in open *Sphagnum* lawns. *Pirata piscatorius* (Figure 48; **Lycosidae**) lives in very wet areas of *Sphagnum* bogs, where the females build a vertical silken tube in the moss, leading down beneath the water surface and providing an escape when the spider is disturbed.



Figure 47. *Erigone welchi* (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.



Figure 48. *Pirata piscatorius* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Komposch (2000) demonstrated the uniqueness of spider **coenoses** of bogs in the wetlands of Austria. He used pitfall traps, light traps, soil sifters, and hand collections to assess the spider fauna of alder forest, willow shrub, hay meadow, moist meadow, sedge swamp, reed bed, meadowsweet fen, floating mat, and raised bog. The dendrogram of communities showed the greatest separation of the bog spiders from those of all other habitats in the study. Nevertheless, the three dominant species were not specialists. *Pirata hygrophilus* (Figure 49; **Lycosidae**) was the most frequent species in the area, but it has a widespread habitat range, including the ground layer of damp woodlands, raised bogs, lowland heaths, marshy grassland, but especially associated with open water (Harvey *et al.* 2002). *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**) was the most abundant and is known from woodland, grassland, heathland and industrial sites, hiding under stones and logs; it prefers dry, heathy conditions to bogs and marshes (Harvey *et al.* 2002). Only *T. spinipalpis* (Figure 22) among these abundant spiders prefers damp places, but even it occurs widely in bogs, wet heath, damp meadows, fens, and marshland. On the Austrian raised bogs, *Trochosa terricola* (Figure 20-Figure 21) and *T. spinipalpis* were **sympatric** (have overlapping distributions) and formed the spider coenosis there. The floating mat bog seemed to be the preferred habitat for *Pirata piscatorius* (Figure 48).



Figure 49. *Pirata hygrophilus* (**Lycosidae**) female with egg sac. Photo by Jørgen Lissner, with permission.

Stewart (2001) sheds light on the niche questions for some of these bog species from Flanders Moss, Scotland. Species that were common in some areas seemed to be absent in many others. This is the case for *Clubiona diversa* (Figure 50; **Clubionidae**), a common bog dweller in Scotland, but preferring drier sites in southern England (Stewart 2001); in Denmark it is common in wet and dry heathland, but not in places with a peat layer. But what is it that causes these spiders to inhabit such disparate habitats in different places?

In Poland, Kupryjanowicz *et al.* (1998) found that the rarest species and those that could be labelled tyrophobionts were present on the more sunlit peat bogs. Among the most numerous of these rare species were **Gnaphosidae**: *Gnaphosa microps* (Figure 26); **Linyphiidae**: *Glyphesis cottonae* (Figure 41) and *Meioneta mossica*; **Liocranidae**: *Scotina palliardi*; **Lycosidae**: *Arctosa alpigena lamperti* (Figure 51), *Pardosa hyperborea* (Figure 52), and *P. maisa* [also from *Sphagnum* in poor pine fens (Itaemies & Jarva 1983)]; **Salticidae**: *Heliophanus dampfi* (Figure 32) and *Cobanus cambridgei*? (as *Talavera westringi*; see Platnick 2013); and **Theridiidae**: *Theonoe minutissima* (Figure 35). But in the mountains of the UK, *Arctosa alpigena* lives both in and under the moss *Racomitrium lanuginosum*. And *Theonoe minutissima* occurs among mosses in woods of the Tyne Valley, UK (Jackson 1906) and in peat bogs as well as among stony debris in North Bohemia (Růžička & Jaher 1996). Other rare species in Poland bogs included **Clubionidae**: *Clubiona norvegica* (Figure 34 – also in moorland in the UK); **Gnaphosidae**: *Haplodrassus moderatus* (Figure 53 – also in mosses of forests in Denmark) and *Zelotes aeneus* (Figure 54); **Linyphiidae**: *Aphileta misera* (Figure 36 – also in marshes in the UK), *Centromerus semiater* (Figure 55), and *Ceraticelus bulbosus* (as *Ceraticelus sibiricus*) (Figure 56); **Lycosidae**: *Pirata insularis*, *P. tenuitarsis* (Figure 10 – also in marshes in Poland), and *Zora armillata* (Figure 57); and **Mimetidae**: *Ero cambridgei* (Figure 58-Figure 59). The percentage of rare species ranged from 3.5% to 18.3%.



Figure 51. *Arctosa alpigena lamperti* (**Lycosidae**) on *Sphagnum*. Photo by Rudolf Macek, with permission.



Figure 52. *Pardosa hyperborea* (**Lycosidae**) on *Sphagnum*. Photo by Tom Murray, BugGuide, through Creative Commons.



Figure 50. *Clubiona diversa* (**Clubionidae**) on dead moss. Photo through Creative Commons.



Figure 53. The nocturnal ground spider, *Haplodrassus moderatus* (**Gnaphosidae**) (7 mm), has been recorded from a range of damp habitats, ranging from moist unimproved grassland (e.g. *Molinia* meadows) to fairly dry *Sphagnum* bogs, such as degraded raised bogs. Photo by Jørgen Lissner, with permission.



Figure 54. *Zelotes aeneus* (Gnaphosidae). Photo ©Pierre Oger, with permission.



Figure 57. *Zora armillata* (Zoridae). Photo by Rudolf Macek, with permission.



Figure 55. *Centromerus semiater* (Linyphiidae) habitus. Photo by Glenn Halvor Morka, with permission.



Figure 58. *Ero cambridgei* (Mimetidae) on leaf. Photo by Jørgen Lissner, with permission.



Figure 56. *Ceraticelus bulbosus* (Linyphiidae). Photo by Chuck Parker, through Creative Commons.



Figure 59. *Ero cambridgei* (Mimetidae) on leaf. Photo by Jørgen Lissner, with permission.

Mosses as Spider Habitats in Bogs and Fens

Is *Sphagnum* Special?

One factor that creates tyrphobionts is having a special requirement. For example, *Pirata hygrophilus* (Figure 23;

Lycosidae is a prominent species in a number of European bogs (Casemir 1976; van Helsdingen 1976; Almquist 1984; Kupryjanowicz *et al.* 1998; Svaton & Pridavka 2000). Unlike the sun-loving rare species described by Kupryjanowicz *et al.* (1998), *Pirata hygrophilus* seems to occur only in areas of shaded *Sphagnum* (Nørgaard 1952). *Pirata piscatorius* (Figure 48) also seems to be confined to the *Sphagnum* area of the habitat (Bruun & Toft 2004).

Some species seem to require the bogs for their winter retreat (Boyce 2004). For example, *Sitticus floricola* (Figure 38; **Salticidae**) spends the winter deep in the *Sphagnum* hummocks (Harvey *et al.* 2002; Boyce 2004).

Boyce (2004) found that for some species, the acid nature of the habitat seemed to be important, but was it the pH (acidity) or the vegetation associated with it? For example, *Hilaira pervicax* (Figure 62; **Linyphiidae**) is an acid mire dweller among *Sphagnum* and rushes in acid flushes and blanket mires (Boyce 2004). *Hilaira nubigena* (Figure 30) lives above 400 m and is likewise associated with *Sphagnum* and rushes in acid flushes and blanket mires. *Semljicola caliginosus* (**Linyphiidae**) lives in *Sphagnum* and wet litter on blanket mires. *Clubiona norvegica* (Figure 34; **Clubionidae**), *Walckenaeria kochi*, (Figure 61) and *W. clavicornis* (Figure 63; **Linyphiidae**) are primarily known from acid (*Sphagnum*) mires in Britain, but they are not restricted to this habitat (see Chapter 7-2). *Pirata tenuitarsis* (Figure 10; **Lycosidae**) usually lives among *Sphagnum* near bog pools. Do they require this habitat, or do they benefit from lack of a predator or competing species?



Figure 60. *Sitticus floricola* (**Salticidae**). Photo by Peter Harvey, Spider Recording Scheme-British Arachnological Society.



Figure 61. *Walckenaeria kochi* on *Polytrichum* sp. Photo by Rudolf Macek, with permission.



Figure 62. *Hilaira pervicax* (**Linyphiidae**). Photo by Marko Mutanen, through Creative Commons.



Figure 63. *Walckenaeria clavicornis* (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.

On the other hand, some spider species prefer *Sphagnum* habitats, but are not necessarily confined to bogs. At the Lesni Lom Quarry (Brno-Hady) in the Czech Republic, *Zelotes clivicola* (Figure 64; **Gnaphosidae**) was abundant among mosses in peat bogs, but it also occurred under stones in peat bogs and among mosses in pine and birch forests (Hula & Štátna 2010).



Figure 64. *Zelotes clivicola* (**Gnaphosidae**) male. Photo by Jørgen Lissner, with permission.

Maelfait *et al.* (1995) found that *Gongylidiellum latebricola* (Figure 65; **Linyphiidae**) was one such species, with its presence correlating with the presence of *Sphagnum* in riverine forests in Flanders, Belgium. But what is the role of *Sphagnum* in such habitats? Is it a winter retreat? Or could it be a moist refuge in the heat or drought of summer? I (Lissner) have found it commonly among *Hypnum* mats in forests in Denmark and about equally common from acidic fens (with or without *Sphagnum*). Hence, whatever role *Sphagnum* has for this species, it is apparently not unique. Furthermore, not all *Sphagnum* species are equal, with some occurring in forests in shallow turfs, some submerged, and others at varying water levels in the open.

In Russia, two members of **Lycosidae**, *Pardosa atrata* and *Pirata piscatorius* (Figure 48), occur commonly in bogs, but are absent from forests (Oliger 2004). *Antistea elegans* (Figure 9; **Hahniidae**), *Gnaphosa nigerrima* (Figure 12; **Gnaphosidae**), and *Arctosa alpigena* (Figure 51; **Lycosidae**) (as *Tricca alpigena*) were numerous in bogs, rare in forests. On the other hand, four **Lycosidae** were dominant in both bogs (48%) and forests (52%) in this study: *Alopecosa pulverulenta* (Figure 66), *Pardosa sphagnicola* (Figure 8), *P. hyperborea* (Figure 52), and *Pirata uliginosus* (Figure 33).



Figure 65. *Gongylidiellum latebricola* (**Linyphiidae**) on moss. Photo by Jørgen Lissner, with permission.



Figure 66. *Alopecosa pulverulenta* (**Lycosidae**) with spiderlings on moss. Photo by Walter Pfliegler, with permission.

Pommeresche (2002) found that bog spider communities in Norway had more species in common with the open *Calluna*-pine forests than with other types of forests, perhaps indicating an acid preference. **Lycosidae**, **Liocranidae**, and **Tetragnathidae**, for example, dominated both bogs and *Calluna*-pine forests. Some species indicated open areas: *Trochosa terricola* (Figure 20-Figure 21; **Lycosidae**), *Gonatium rubens* (Figure 67; **Linyphiidae**), and *Pardosa pullata* (Figure 18-Figure 19; **Lycosidae**). *Pirata hygrophilus* (Figure 23; **Lycosidae**) was an indicator species for bogs. *Pirata hygrophilus* and *Notioscopus sarcinatus* (Figure 27; **Linyphiidae**) (in wet *Sphagnum* and *Polytrichum* under scrub) only occurred in the bogs, whereas elsewhere in Europe *P. hygrophilus* frequently occurs in humid forests (Maelfait *et al.* 1995; Thaler 1997) and *Notioscopus sarcinatus* (Figure 68) occurs in fens (Boyce 2004), supporting the observation that the preferred habitat may differ geographically.



Figure 67. *Gonatium rubens* (**Linyphiidae**). Photo by James K. Lindsey, with permission.



Figure 68. *Notioscopus sarcinatus* on moss. Photo by Jørgen Lissner, with permission.

Heathlands, another acid habitat, have some species exclusively in common with the bog habitats. For example, *Hypselistes jacksoni* (Figure 69; **Linyphiidae**) and *Trochosa spinipalpis* (Figure 22; **Lycosidae**) occur almost exclusively in bogs and wet heaths in Great Britain (Boyce 2004).



Figure 69. *Hypselistes jacksoni* (Linyphiidae) on moss. Photo by Jørgen Lissner, with permission.

As might be expected, marshlands can have similar species to those of bogs. *Gnaphosa nigerrima* (Figure 12; Gnaphosidae) occurs in *Sphagnum* lawns (Boyce 2004) as well as in marshes (Kupryjanowicz 2003). On the other hand, *Carorita limnaea* (Figure 70; Linyphiidae) not only lives in very wet acid *Sphagnum* mires (Boyce 2004), but also in mixed coniferous woods (Pickavance & Dondale 2005), another typically acid habitat.



Figure 70. *Carorita limnaea* (Linyphiidae) suspended from moss. Photo by Jørgen Lissner, with permission.

The foregoing studies imply the importance of the vegetation structure, at least as a complement to the niche provided by *Sphagnum*. But how do we explain that some spider species occur in what appear to be very different habitats? For example, *Satlatlas britteni* (Linyphiidae) lives in *Sphagnum* bogs and salt marshes (Boyce 2004). In the Faroe Islands, *Centromerita bicolor* (Figure 71; Linyphiidae) not only occurs in *Sphagnum* wetlands, but also on a sand dune, as well as many other habitat types (Lissner 2011). Clearly some of these are generalists, but some, like *Satlatlas britteni* occupy only two very different habitats.



Figure 71. *Centromerita bicolor* on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.

The Bog and Fen Habitat

Hummocks and Hollows

Topogenous *Sphagnum*-dominated, acidic fens are frequently developed into a topographic mosaic of hollows and hummocks. Hollows only provide a thin layer of non-flooded moss as habitat and may become seasonally flooded. Hummocks provide a deeper layer of moss/peat, including subsurface air spaces that spiders may occupy. Not surprisingly, a higher number of spider species is associated with the hummocks than in the surrounding hollows, at least when it comes to spiders living within the moss layer (Koponen 2004). Hummocks are less susceptible to flooding and provide more stable environments than the hollows. The structures of hummocks are more complex due to the thickness of the moss layer and the presence of a higher number of moss and plant species. Thus, they offer lots of hiding and hunting places per unit of area. They may also exhibit a more uniform climate internally except for the upper few centimeters. Ant colonies (e.g. *Formica*, *Myrmica* spp.) are common features of hummocks and the activities of ants may diversify habitats, providing internal runways, and increasing the number of spider species sustained by the hummocks. According to Lesica and Kannowski (1998) the activities of ants may provide an environment for plants that has better aeration and is warmer, as well as nutrient-enriched, allowing more plant species to colonize the hummock. This undoubtedly affects the properties of the spider habitats. Cavities produced by ants may be exploited by web-building spiders, e.g. the small comb-footed spider, *Theonoe minutissima* (Figure 35; Theridiidae), a spider mostly found within hummocks. Densities in moist hollows, low hummocks, and higher *Sphagnum fuscum* hummocks are 1.7-2.1- fold higher than in wet hollows (Koponen 2004). *Drepanotylus uncutus* and *Pardosa sphagnicola* were more abundant in moist hollows in southern Finland and *Robertus arundineti* in hummocks.

Indirect Association with *Sphagnum*

Many spiders found in bogs and fens are indirectly associated with mosses. For example the stunted trees sometimes found on open or scarcely wooded ombrogenous bogs or on poor fens provide microhabitats suitable for spiders (Figure 72). Usually they contain plenty of loose bark and rotten wood, much preferred

hiding places for many spider species. The orb weaver *Araneus marmoreus* (Figure 73-Figure 75; **Araneidae**) is frequently found in wooded wetlands, constructing its web usually at heights above 1.5 m (Harvey *et al.* 2002). The long-jawed orb weaver, *Tetragnatha nigrita* (Figure 76; **Tetragnathidae**), is largely confined to branches of birch and other trees growing on *Sphagnum* bogs and fens, and is only rarely found on the same tree species growing outside bogs and fens. The spider fauna associated with the herb layer of bogs and fens is also distinctly different from that of the herb layer of nearby drier places. For example, the jumping spider *Heliophanus dampfi* (Figure 32; **Salticidae**) can be swept from the herb layer and from tree saplings in *Sphagnum* bogs, but is very rare in other types of wetlands.



Figure 72. *Sphagnum* bog with stunted birch, near Lake Salten Langsø, Denmark. Photo by Jørgen Lissner, with permission.



Figure 73. *Araneus marmoreus* (**Araneidae**) showing disruptive coloration. Photo by Trevor and Dilys Pendleton <<http://www.eakringbirds.com/>>, with permission.



Figure 74. *Araneus marmoreus pyramidatus* (**Araneidae**) on moss at Hatfield Moors. Photo by Brian Eversham, with permission.



Figure 75. *Araneus marmoreus* (**Araneidae**) showing pyramid design on the dorsal side of the abdomen. Photo by Jørgen Lissner, with permission.



Figure 76. *Tetragnatha nigrita* (**Tetragnathidae**) female on leaf. Note the abdominal patterning that resembles that of dead leaves. Photo by Walter Pfliegler, with permission.

Differences among Bogs and Fens

Individual **ombrogenous** (dependent on rain for its formation) bogs as well as poor fens seem to possess rather different spider assemblages even if located relatively close to one another. Many moss-associated spider species of the bogs appear to have a very scattered distribution, being found only in a few widely separated bogs, e.g. *Robertus unguulatus* (Figure 77; **Theridiidae**), *Clubiona norvegica* (Figure 34; **Clubionidae**), *Glyphesis cottonae* (Figure 41; **Linyphiidae**), and *Carorita limnaea* (Figure 70; **Linyphiidae**). This is puzzling since the dispersal capacity usually is high for spiders. Perhaps this is a combination of low dispersal capacity, inhospitable land between sites, and local extinction exceeding recolonization.



Figure 77. *Robertus unguulatus* male on moss. Photo by Jørgen Lissner, with permission.

One of the spiders that seems to prefer the *Sphagnum* habitat is *Pardosa sphagnicola* (Figure 79-Figure 81; **Lycosidae**; Oliger 2004). In the Lake Ladoga region of Russia, this species is the most abundant and is nearly ubiquitous among the peatlands. Oliger found that there was significant similarity in the taxa of spiders in peatlands in NW Russia, Finland, and Lithuania. These especially included **Lycosidae**, **Gnaphosidae**, and **Liocranidae**. The latter were frequently encountered in pitfall traps.



Figure 78. *Pardosa sphagnicola* (**Lycosidae**) on *Sphagnum*. Photo by Barbara Thaler-Knoflach, with permission.



Figure 79. Male *Pardosa sphagnicola* (**Lycosidae**), an inhabitant of *Sphagnum*. Photo by James K. Lindsey, through Wikimedia Commons.



Figure 80. *Pardosa sphagnicola* (**Lycosidae**) female with egg sac. Photo by James K. Lindsey, through Wikimedia Commons.



Figure 81. *Pardosa sphagnicola* (**Lycosidae**) female with spiderlings among *Sphagnum* branches. Photo by James K. Lindsey, through Wikimedia Commons.

Niche Separation – Lycosidae

Nørgaard (1951) reported on the common lycosid spiders *Pardosa pullata* (as *Lycosa pullata*; Figure 82; **Lycosidae**) and *Pirata piraticus* (Figure 83; **Lycosidae**) in Danish *Sphagnum* bogs. These two spiders live in close proximity to each other, but their microdistribution

vertically is very different. *Pardosa pullata* (4-6 mm length) prefers moist habitats, where it runs about on the surface of the closely knit *Sphagnum* capitula (plant tops; Figure 1), although in Great Britain the maritime climate permits it to be quite ubiquitous. In Denmark, Nørgaard found a mean of 12 individuals per square meter on the surface of the *Sphagnum* carpet in mid July. *Pirata piraticus* (up to 9 mm long; Figure 83) likewise prefers moist habitats. Stewart (2001) considers *Pirata piraticus* to be the commonest wolf spider of wet, marshy areas with *Sphagnum* moss, where it dwells beneath the surface among the much more open realm of *Sphagnum* stems (Nørgaard 1951). Nevertheless, it stays close to a free water surface (Nørgaard 1951). As discussed above, temperature can account for the separation of these two species. In the topographic depression bog used for this study, daily air temperatures vary widely from 6°C at night (due to cold air masses streaming down from higher ground) to 32°C in the daytime sun (Figure 84). At the *Sphagnum* surface it is even higher, reaching 39°C. Such wide variation is not, however, the case among the stems within the *Sphagnum* mat. During the same time period, temperatures ranged only 17 to 22°C at 10 cm below the surface.



Figure 82. *Pardosa pullata* (Lycosidae) female on *Sphagnum*. Photo by Jørgen Lissner, with permission.



Figure 83. *Pirata piraticus* (Lycosidae) male. Photo by Jørgen Lissner, with permission.

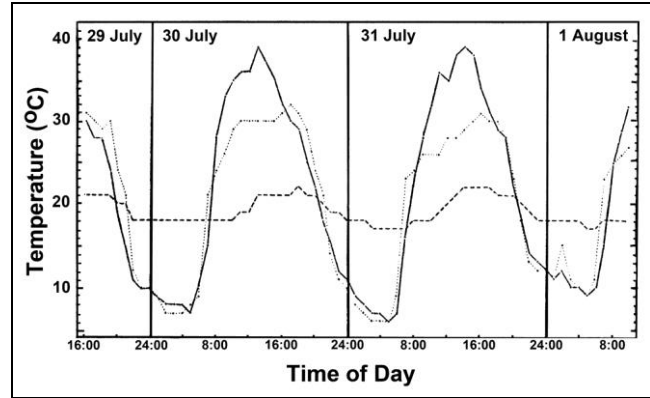


Figure 84. Daily fluctuations in temperature during mid summer in a *Sphagnum* bog in Denmark at 10 cm below surface (---), surface (—), and 100 cm above surface (.....). Redrawn from Nørgaard 1951.

Further separation of the two species is provided by the differences in relative humidity, especially in summer. During the three days at the end of July when the temperature was measured, the humidity at the surface where *Pardosa pullata* (Figure 82) resides dropped to as low as 40% in the daytime (Nørgaard 1951). On the other hand, the stem layer habitat of *Pirata piraticus* (Figure 83) remained a constant 100%. In experiments, Nørgaard demonstrated that *P. pullata* has a greater tolerance for low humidity than does *P. piraticus*. The former species had 100% survival for the 8 hours of the experiment at ≥85% humidity in the temperature range of 20-35°C, whereas *P. piraticus* survived only 2.5 hours at 85% humidity. At lower humidity levels (64 & 43%), *P. piraticus* generally did not survive for 8 hours at any of these temperatures.

For these two spider species, the life cycle is closely tuned to the conditions of the bog (Nørgaard 1951). Both species hibernate while they are still immature. *Pardosa pullata* (Figure 82) hibernates in tussocks of rush, sedge, and *Polytrichum* turfs (Figure 85). These locations keep it safely above the water surface even during winter floods. In spring the female carries its egg cocoon attached to its spinnerets. This species spends its days running about the *Sphagnum* surface, particularly while the sun is shining. It can hide from enemies among the irregularities of the carpet and hunches up between the capitula at night and during cold spells, never entering the stalk layer. Both males and females have disappeared by mid September.



Figure 85. Bog with *Polytrichum* cushions. Photo by James K. Lindsey, with permission.

Pirata piraticus (Figure 83) actually survives in an active state through the winter (Figure 86) and must face some severe conditions. Nørgaard (1951) observed young *P. piraticus* under the frozen *Sphagnum* capitula (Figure 86). Although their movements when disturbed in the field were sluggish, they became quite active when the clumps of moss were thawed in the lab. In this species, the female spider builds a retreat tube vertically in the stem layer (Figure 87). This tube is 6-8 cm tall and open at both ends. The upper end opens at the surface of the *Sphagnum* carpet. The eggs are deposited in the tube and wrapped in a spherical dirty-white cocoon, still attached to the spinnerets. The female takes advantage of the upper opening to position her attached eggs at the surface on sunny days. Disturbance causes the visible cocoons to disappear into the retreat as the female responds to the motion. If they are further persecuted, they exit the tube at the lower end and run on the water surface until they can find a stem to climb down below the water surface.



Figure 86. *Sphagnum squarrosum* showing frosted branches during early winter. Photo by Michael Lüth, with permission.

It appears that the location of the tube among the *Sphagnum* stems is ideal for the female spider to incubate her eggs. Nørgaard (1951) experimented with the temperature preferences of newly captured *Pirata piraticus* (Figure 83) and found that both males and females without cocoons preferred temperatures of 18-24°C. However, when the females had egg cocoons, their temperature preference changed to 26°-32°C. By positioning themselves upside down in the tube with the egg cocoon at the surface of the *Sphagnum*, the females could maintain a comfortable body temperature while keeping the eggs at their needed higher temperature. Nørgaard also determined that the temperature was more important than the humidity. In a strong temperature gradient, the spiders would go to 21°C in a moist area or a dry area, depending on where that temperature was available. By contrast, *Pardosa pullata* (Figure 82) does not change its temperature preference when carrying egg cocoons and prefers temperatures of 28°-36°C, making the surface of the *Sphagnum* its location of choice.

Temperature further plays a role in mortality. In the experiments by Nørgaard (1951), *Pirata piraticus* (Figure 83) suffered heat stupor at 35°-36°C, whereas *Pardosa pullata* (Figure 82) experienced heat stupor at 43°C. It is interesting that *Pardosa pullata* females with cocoons began normal movements at 12-14°C, whereas *Pirata piraticus* began at 14-19°C. Clearly the spaces among

Sphagnum stems provide the buffered temperature range that is necessary for the life cycle of *Pirata piraticus*. Nørgaard suggests that construction of the tube permits *Pirata piraticus* to move more quickly to the deeper, cooler part of the mat than would movement through the capitulum layer from the surface of the *Sphagnum* mat when the temperature at the surface approaches the spider's lethal temperature. Even though adults in this family may be too large to move easily among bryophytes, juveniles may find this habitat ideal.

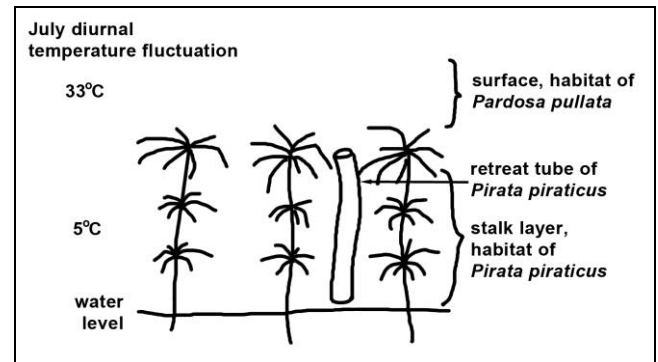


Figure 87. Comparison of temperature niches of two Lycosidae spiders from Danish *Sphagnum* bogs. Based on Nørgaard 1951.

Bryophytes and Trap-door Spiders

Bog habitats are also home to some trap-door spiders (Ctenizidae) that lie in wait for their prey. They make themselves inconspicuous by hiding in a burrow with a trap-door opening (Cloudsley-Thompson 1989). These trap doors are often further camouflaged by bits of lichen or moss incorporated into them.

Bryophytes Hide New Species

Reports describing new species can provide additional species that live in boggy habitats, sometimes giving more detailed habitat information. Efimik and Eshunin (1996) described *Walckenaeria korobeinikovi* (Figure 88; Linyphiidae) as a new species from a boggy habitat in the Urals. Palmgren (1982) described the ecology of *Walckenaeria alticeps* (Figure 89) as new to Finland, where it is restricted to very wet, deep *Sphagnum* or wet debris in areas with some canopy cover. We should expect to find more species as researchers look more carefully at the multiple layers of the bryophytes in bogs and fens.



Figure 88. *Walckenaeria korobeinikovi* (Linyphiidae). Photo by Gergin Glagoev through Bold Systems, through Creative Commons.



Figure 89. *Walckenaeria alticeps* (Linyphiidae) male on *Sphagnum*. Photo by Jørgen Lissner, with permission.

It appears that a *Racomitrium* hummock in the middle of a *Sphagnum* bog can afford a different habitat from its surroundings. For example, *Micaria alpina* (Figure 90; Gnaphosidae) occurs among grass, moss, and under stones above 750 m in Great Britain, but it also is known from a *Racomitrium* hummock (Figure 91) in the middle of a *Sphagnum* bog (Harvey *et al.* 2002).



Figure 90. *Micaria alpina* (Gnaphosidae) female. Photo by Walter Pfliegler, with permission.



Figure 91. *Racomitrium lanuginosum* hummock, refuge for spiders above the water. Photo by Peter J. Foss <<http://www.fossenvironmentalconsulting.com/>>, with permission.

Conservation Issues

When peatlands are endangered, so are their spiders. The spider species are as unique as those of the plants (Bruun & Toft 2004). Scott *et al.* (2006) found that the number of spider bog indicator species can serve as a surrogate for conservation value of the total invertebrate fauna of bogs. They used three parameters to assess their indicator value: naturalness index, species quality, and species rarity curve. The **naturalness index** has a scale of 1-10, with 0 being totally artificial (Machado 2004). The **species quality index** requires assigning a numerical score to all species present according to their rarity. The index is equal to the sum of the quality scores divided by the number of species. Scott *et al.* used the Red Data Book classification as indicated in Harvey *et al.* (2002) to develop those assignments. These categories were assigned as follows: Common = 1, Local = 2, Notable B = 4, Notable A = 8, RDB3 = 16, RDB2 = 32 and RDB1 = 64. For example, *Heliophanus dampfi* (Figure 32; Salticidae) was assigned 32 points and *Gnaphosa nigerrima* (Figure 12; Gnaphosidae), the rarest species, 64 points (Harvey *et al.* 2002). The **species-area curve** indicates the steepness of the curve as each species is added to the list. In developing their criteria for indicator species, they considered that three criteria must be met to indicate a good indicator species of a good peatland site:

1. the naturalness index exceeds 0.5
2. the species quality is greater than 2.8
3. the indicator species-area relationship is above the trend line (see Figure 92).

Hence, tracking spider fluctuations can serve as a warning system for peatlands in decline.

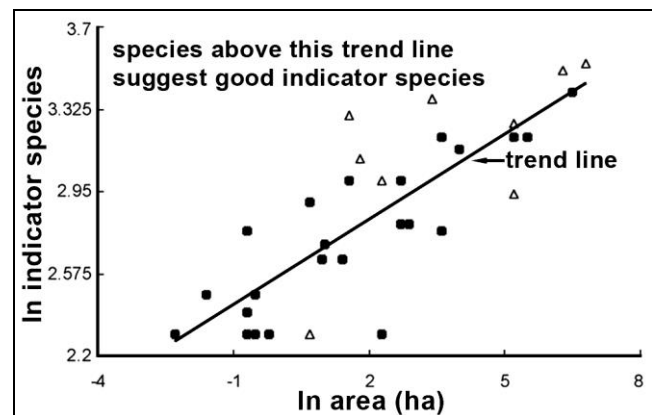


Figure 92. Species-area curve for spiders from 32 bogs in western Britain. Redrawn from Scott *et al.* 2006.

Platen (2004) demonstrated that spider communities can be used to assess the state of degradation of oligotrophic moors. DECORANA demonstrated differences between the lowest and highest stages of degradation, but failed to distinguish the four stages between those. Platen attributed this to the predominance of eurytopic species occurring in the middle stages. However, the Kruskal-Wallis test did discriminate among all the stages. Forest species increased with increasing degradation. Typical species of oligotrophic moors (less hygrophilic) had the greatest abundance at medium stages of degradation.

Peatland Fire Communities

Studies indicate that loss of peatlands can precipitate a serious loss of spider species. As seen above, a number of rare species occur in bogs and fens. In the following example, fire destroyed the peatland of Sudas Bog in Latvia and this study examined the spider fauna the first season afterwards (Spuðgis *et al.* 2005). A surprisingly large number of species (48), compared to 40 in the unburned areas, occupied the peatlands after this short time. The invading community was somewhat different from the previous peatland community. The dominant colonizers were *Agroeca proxima* (Figure 93; **Liocranidae**), a species typical of pine bogs (Koponen *et al.* 2001; Rēlys *et al.* 2002), and *Alopecosa aculeata* (Figure 94; **Lycosidae**), two species with good mobility. Nevertheless, most of the species were typical of the original pine bog. Activity levels likewise were similar to those on the unburned bog. It is possible that some of these species were able to survive the fire from deep within the moss layer, but many colonized from the surrounding bog habitats, possibly travelling up to 120 m.

One interesting phenomenon was that the spiders, even though they were the same species, were darker in color in the burned over bog (Spuðgis *et al.* 2005). This was especially true in *Ozyptila trux* (Figure 95; **Linyphiidae**), a slow-moving spider (Stewart 2001) that probably survived the fire. Spuðgis and coworkers suggested that this darker color was in response to the dark color of the burned peat, perhaps due to greater predation on more visible light-colored individuals. It is also possible that more dark-colored individuals survived the increased exposure to UV light better.



Figure 93. *Agroeca proxima* on moss. Photo by Jørgen Lissner, with permission.



Figure 94. *Alopecosa aculeata* (**Lycosidae**) female from under moss. Photo by John Sloan, with permission.



Figure 95. *Ozyptila trux* (**Linyphiidae**) male among mosses. This species is darker in burned areas. Photo by Jørgen Lissner, with permission.

The **Gnaphosidae**, with *Drassyllus pusillus* (Figure 96), *Gnaphosa microps* (Figure 26), and *Zelotes latreillei* (Figure 97) typically occurring in unburned bogs, were notably absent after the fire (Spuðgis *et al.* 2005). Typical species that colonized and were also present in the unburned bogs included *Trochosa spinipalpis* (Figure 22; **Lycosidae**) and *Oryphantes angulatus* (Figure 98; **Linyphiidae**) from various depths of *Sphagnum*, *Agroeca proxima* (Figure 93; **Liocranidae**), *Alopecosa aculeata* (Figure 94; **Lycosidae**) [also known after fire in Canada (Aitchison-Benell 1994)], and *Euryopis flavomaculata* (Figure 99; **Theridiidae**) (another slow-moving spider that probably survived the fire). Species such as the **Linyphiidae** *Agyneta cauta*, *Micrargus apertus* (Figure 100), and *Oryphantes angulatus*, and *Robertus lividus* (Figure 101; **Theridiidae**), live in deep layers of moss and probably are able to survive fire (Spuðgis *et al.* 2005). *Agyneta cauta* (**Linyphiidae**), *Tenuiphantes cristatus* (Figure 102; **Linyphiidae**), *Phrurolithus festivus* (Figure 103; **Corinnidae**), *Alopecosa pulverulenta* (Figure 104; **Lycosidae**), and *Hygrolycosa rubrofasciata* (Figure 105; **Lycosidae**) are active in the upper layer of *Sphagnum*, but it is possible that they likewise retreated deep into the moss to escape the heat and dryness of the fire. *Gnaphosa bicolor* (Figure 106; **Gnaphosidae**) and *Porrhomma pallidum* (Figure 107; **Linyphiidae**) were probably early invaders – they are species not typical of peatland. *Aulonia albigera* (Figure 108; **Lycosidae**) is likewise a probable invader; its activity is restricted to the surface except for its retreat in *Sphagnum* (Spuðgis *et al.* 2005). The tiny **Linyphiidae** most likely were least able to survive the fire (Hauge & Kvamme 1983); their small size would make them gain heat faster and lose water faster, at the same time preventing them from moving very far. All things considered, the colonizers, whether from outside or from deep in the peat, are still mostly species typical of peat bogs. This is partly because many of the peatland species are actually xerothermic, capable of surviving the dry summer periods.



Figure 96. *Drassylus pusillus*. Photo by Rudolf Macek, with permission.



Figure 97. *Zelotes latreillei* (Gnaphosidae). Photo by James K. Lindsey, with permission.

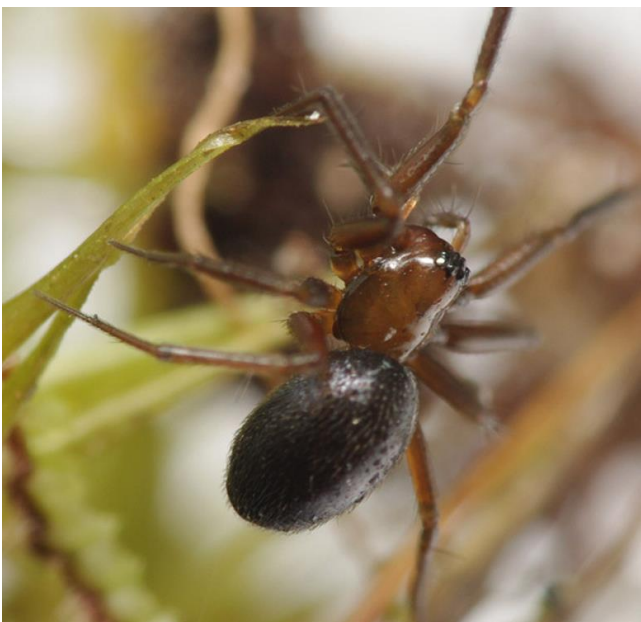


Figure 98. *Oryphantes angulatus* (Linyphiidae) female on moss. Photo by Walter Pfliegler, with permission.



Figure 99. *Euryopsis flavomaculata* (Theridiidae). Photo by Glenn Halvor Morka, with permission.



Figure 100. *Micrargus apertus* (Linyphiidae). Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 101. *Robertus lividus* female among mosses. Photo by Jørgen Lissner, with permission.



Figure 102. *Tenuiphantes cristatus* (Linyphiidae) male on litter. Photo by Walter Pfliegler, with permission.



Figure 103. *Phrurolithus festinus* (Corinnidae) on moss. Photo by Jørgen Lissner, with permission.



Figure 104. *Alopecosa pulverulenta* (Lycosidae) male. Photo by James K. Lindsey, with permission.



Figure 105. *Hygrolycosa rubrofasciata* (Lycosidae) on moss. Photo by Arno Grabolle <www.arnograbolle.de>, with permission.



Figure 106. *Gnaphosa bicolor* (Gnaphosidae) male on moss. Photo by Jørgen Lissner, with permission.



Figure 107. *Porrhomma pallidum* (Linyphiidae) female live on *Sphagnum*. Photo by Glenn Halvor Morka, with permission.



Figure 108. *Aulonia albirana* (Lycosidae) on moss. Photo ©Pierre Oger, with permission.

In the taiga of southeastern Manitoba, Canada, pitfall traps revealed similar trends to those in Latvia for spider communities of burned and unburned bogs. As in Sudas Bog in Latvia, there were more species in the burned bog after the fire (Aitchison-Benell 1994). The numbers of species remained high for about two months after the fire, then decreased, as one might expect for the usual seasonal activity patterns. In this case, 50 spider species were located in the burned plots and only 45 in the control plots, with 26 species common to both. Species present in burned plots but not in the control bogs included **Lycosidae**: four species of *Pardosa*, *Alopecosa aculeata* (Figure 94), and *Trochosa terricola* (Figure 20-Figure 21); **Liocranidae**: *Agroeca ornata* (Figure 109); **Linyphiidae**: *Bathyphantes pallidus* (Figure 110), *Erigone atra* (Figure 111), *Pocadicnemis americana* (Figure 112), and *Tunagyna debilis* (Figure 113). The control bogs also had unique species that apparently were unable to survive the fire: *Hogna frondicola* (Figure 114; **Lycosidae**); *Gnaphosa microps* (Figure 26Figure 26; **Gnaphosidae**), and *Neoantistea agilis* (Figure 115; **Hahniidae**). *Gnaphosa microps* likewise disappeared after fire in Latvian bogs (Spuõgis *et al.* 2005).



Figure 111. *Erigone atra* maneuvering among the dead portions of mosses. Photo by Jørgen Lissner, with permission.



Figure 109. *Agroeca ornata* male. Photo by Yann Gobeil, through Creative Commons.



Figure 112. *Pocadicnemis americana*. Photo by Gergin Blagoev, through Creative Commons.



Figure 110. *Bathyphantes pallidus* (Linyphiidae) female. Photo by Tom Murray, through Creative Commons.



Figure 113. *Tunagyna debilis*. Photo by Bold Systems Biodiversity Institute of Ontario, through Creative Commons.



Figure 114. *Hogna frondicola* (Lycosidae). Photo by Steve McKechnie, through Creative Commons.



Figure 115. *Neoantistea agilis* (Hahniidae) male on leaf. Photo by Tom Murray, through Creative Commons.

Maintenance, and even increases, of species richness after fire seem to be common trends among spiders of various habitats (e.g. Aitchison-Benell 1994; Neet 1996; Spuògis *et al.* 2005). But Neet points out that early assessment can be misleading, as seen in the Manitoba bogs (Aitchison-Benell 1994). Rare species that survive in the habitat before a fire can disappear as invading species replace them (Neet 1996).

Larrivée *et al.* (2005) clarified some of the disturbance relationships in a Canadian black spruce (*Picea mariana*) forest. Although this was not a bryophyte study, the principles are most likely the same. When comparing clear-cut sites with burned stands, they found that the hunting spiders (Lycosidae) were more abundant in the clear-cut stands. Although the Lycosidae typically increase after fire, spiders in the clear-cut stands would escape the lethal effects of fire and thus may have retained the original species. This suggestion is supported by the high turnover (2X) of these spiders in the burned areas. Web-building spiders had similar catch rates in these two groups of sites and in uncut controls, but surprisingly had the highest turnover rates and gamma diversity. The clearcuts were characterized by spider communities typical of

dry, open, disturbed forest floor, whereas those in burned stands correlated with high cover of shrubs and dried moss-lichen substrate and deep litter, likely refuges during the fire as well as areas of higher moisture after the fire.

Moretti (2000) examined the effects of winter fires in forests of the Alps and found that 30% of the species occurred only in the burned sites, whereas only 7% were exclusive to the unburned controls. The absence of pioneer species in the burned sites suggests that the spiders were able to survive the fire.

Lycosidae are mobile species and thus are able to invade quickly after a fire, as seen by Spuògis *et al.* (2005) for bogs and Koponen (2005) for forests. Linyphiidae, on the other hand, are nearly immobile and may be greatly reduced in numbers after a fire, as seen by Koponen (2005) for a forested site. In bogs, where wet mosses can provide refuge during the fire, Linyphiidae can survive and thus be present after the fire (Spuògis *et al.* 2005). But this family can diminish in numbers in succeeding years, while the Lycosidae can increase (Koponen 2005).

Summary

Bogs and fens house spiders that benefit from the more constant moisture provided, but also from the moderated temperature, shade, food organisms, and refuge from predation. As in many mossy habitats, the Linyphiidae are prominent. But spiders in the Lycosidae – hunting spiders – can be seen running across the water surface or the surface of sunny *Sphagnum*. Nevertheless, many species are xerophiles, living in exposed areas of the bog or fen. The lycosid genera *Arctosa*, *Pirata*, *Pardosa*, and *Trochosa* are widespread in the peatland habitat, but species vary geographically. They are the most conspicuous, but in smaller numbers than the small Linyphiidae. Although there are a few widespread species in the bogs, rare species such as *Heliophanus dampfi* and *Maro lepidus* may be found somewhat frequently here. Few species seem to be **tyrophobionts** (species that are confined to living in peat bogs and mires), and that status seems to differ by country.

Some spiders use *Sphagnum* for a winter retreat. Others seem to benefit from the low pH. Some have only an indirect association, living among the tracheophytes that live in the peatlands. Even within the *Sphagnum* mat, niche separation can occur in the temperature-moisture-light gradient among the stems.

Trap-door spiders cut a door cover in the surface soil-moss layer, where the mosses seem to hold the soil together and permit the hinge to work. The mosses also provide camouflage.

Spiders can be used to assess the naturalness and degradation of peatlands and serve as a surrogate for other invertebrate taxa. Fires in peatlands cause a serious loss of spider species, especially rare species. The invading community is somewhat different from the original peatland community, partly due to lack of a nearby recolonization source. Other species survive the fire among the damp peat, but these may disappear within a few years due to interactions with invading spider species, especially the mobile Lycosidae.

Acknowledgments

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