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Jeffrey C. Nekola
University of Wisconsin

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BUTTERFLY (LEPIDOPTERA: LYCAENIDAE, NYMPHALIDAE, AND SATYRIDAE) FAUNAS OF THREE PEATLAND HABITAT TYPES IN THE LAKE SUPERIOR DRAINAGE BASIN OF WISCONSIN

Jeffrey C. Nekola¹

ABSTRACT

The butterflies which complete their entire life cycle within peatland habitats were documented in the Lake Superior drainage basin of northwestern Wisconsin. Seventy peatlands were inventoried over the course of the 1996 growing season, and were classified as either muskeg, kettlehole, or coastal sites. Muskeg peatlands were of similar elevation to the surrounding uplands, possessed drier and more nutrient-poor substrates, and were typically larger than other peatland types. Kettlehole peatlands were wetter and had floating *Sphagnum* mats which fringed lake margins or were in depressions much lower than the surrounding uplands. Coastal peatlands were located in estuaries along the Lake Superior coast, and possessed relatively eutrophic, wet soils. Muskeg sites harbored the most diverse total fauna, and possessed the highest average number of taxa per site. A highly significant correlation between habitat size and butterfly richness was observed in both muskeg and kettlehole peatlands. The muskeg fauna included five taxa not found in other peatland habitats. These species have arctic-boreal affinities and reach their southern range limit in eastern North America on these sites.

Even though peatlands are moderately frequent and widely distributed across northern Wisconsin, relatively few systematic studies of their biodiversity has been conducted. Curtis (1959) described only a single peatland community type (open bog) in northern Wisconsin, and characterized its vegetation based upon only 17 stands. Contemporary ecological investigations of Wisconsin peatlands have been largely limited to fens in the southeastern counties (e.g., Reed 1985, Carpenter 1990). The first intensive butterfly surveys of northern Wisconsin peatlands (e.g., Ebner 1970, Masters 1971a, 1971b, 1972, Ferge & Kuehn 1976) uncovered a group of boreal and/or arctic taxa (*Clossiana eunomia dawsonii* (Barnes & McDunnough), 1916; *Clossiana freija* (Thunberg), 1791; *Clossiana frigga saga* (Staudinger), 1816; *Erebia discaidalis* (Kirby), 1837; *Oeneis jutta* (Hübner), 1805) which reach the southern limit of their eastern North American range on these sites. However, these studies did not systematically inventory all peatland sites within a region, or compare faunas of different types of peatlands.

Recent ecological analyses of peatlands in northern Minnesota (Glaser 1987) and Michigan (Crum 1992) have documented a great diversity of peat-

¹Department of Natural and Applied Sciences, University of Wisconsin—Green Bay, Green Bay, WI 54311.

lands, ranging from highly minerotrophic fens to ombrotrophic bogs. Based on these investigations it appears that any monolithic view of northern Wisconsin peatlands is an oversimplification. Unpublished plant community, water, and soil chemistry data (Eric Epstein and James Meeker, pers. comm.) suggest that three broad classes of peatland habitats can be recognized in northern Wisconsin. Muskeg sites are dominated by an open Black Spruce (*Picea mariana* (Mill.) BSP.)—*Carex oligosperma* Michx.—*Eriophorum spissum* Fern.—*Sphagnum* savanna, are relatively dry (except in the proximity to moats or bog lakes) and are oligotrophic. These sites usually have an elevation similar to their surrounding uplands. Kettlehole peatlands are much wetter and commonly contain floating *Sphagnum*—Leatherleaf (*Chamaedaphne calyculata* (L.) Moench.) mats. These sites range from very oligotrophic to eutrophic, depending upon the nature of infiltrating groundwater, and typically fringe lakes or occur in depressions much lower than their surrounding uplands. Coastal wetlands, located in estuaries along the Lake Superior Coast, are wet and relatively eutrophic sites dominated by Tamarack (*Larix laricina* (DuRoi) K.Koch) and *Carex lasiocarpa* Ehrh. Acid *Sphagnum*-dominated microhabitats are limited to small islands or ridges typically situated near upland margins.

In conjunction with a Wisconsin Department of Natural Resources (WDNR) investigation of Lake Superior coastal wetlands, butterfly faunas were documented in all accessible peatlands within the Lake Superior drainage basin in Ashland, Bayfield, Douglas, and Iron counties of northwestern Wisconsin. From these data it was possible to assess the faunistic similarities and species diversity patterns between peatland sites, as well as the adult behavior and microsite preferences of individual peatland-obligate species.

METHODS

Site selection. Identification of all high-quality peatlands within or adjacent to the Lake Superior drainage basin was accomplished by a fly-over of the study area on May 20, 1996 in a small aircraft. Approximately 5½ hours of flight time were required to survey the entire region at an altitude of 5000–6000 feet in north-south transects running approximately 6 miles apart. Potential survey sites were marked on USGS topographic quads. Other high-quality sites were identified through review of the Biological Conservation Database (BCD) of the WDNR Bureau of Endangered Resources (WBER). A few additional sites were also recommended by Eric Epstein and others in the staff of the WBER. Through this process a total of 70 sites were selected for inventory: 37 were muskegs, 23 were kettleholes, and 10 were coastal sites. While an attempt was made to inventory all high-quality peatlands within the region, some (like the Kakagon Sloughs) were not surveyed due to difficulty in political and/or physical access.

Sampling. The location in longitude-latitude of each surveyed site was determined through digitization of USGS 7.5 minute topographic quads. The centroid, area and perimeter of each was calculated using the Atlas Draw software package.

Sites were surveyed at approximately 1–2 week intervals throughout the 1996 growing season for a total of 4–6 visits. Visits were made at more frequent intervals early in the season when a number of closely spaced emergences occur. Later in the season when emergences were more temporally separated and when individual populations were in flight for longer periods of time, intervals increased to three weeks. Each visit lasted for 15–90 minutes, depending upon site size. During this time a list was made of all en-

countered butterfly and skipper taxa. Observations were also made of the spatial location of individuals within sites, their preferred areas of occurrence, nectar sources, and oviposition locations. Voucher specimens for most peatland-limited taxa were made from each site. These specimens are housed at the University of Wisconsin—Green Bay.

Cumulative species lists for all taxa which live out their entire life-cycle within peatland habitats (*Clossiana eunomia dawsonii*; *Clossiana freija*; *Clossiana frigga saga*; *Clossiana titania* (Esper), 1793; *Coenonympha inornata* Edwards, 1861; *Erebia discoidalis*, *Incisalia augustinus* (Kirby), 1837; *Lycaena dorcas* Kirby, 1837; *Lycaena epixanthe* (Boisduval & LaConte), 1833; *Oeneis jutta*) were generated. No obligate peatland taxa from the families Hesperidae, Papilionidae, or Pieridae were observed. Throughout this report, nomenclature of Opler and Krizek (1984) has been used for butterflies, and Fernald (1950) for vascular plants.

Site-specific species lists were augmented with any additional reports or collections from the Milwaukee Public Museum or the WBER BCD of species which were not observed during this work, but have been previously documented. Only 5 such occurrences were added to the entire data set. By comparison, 155 individual occurrences of peatland-obligate populations were noted through field sampling.

Data analysis. The frequency of peatland butterfly taxa within each peatland group was measured by counting the total number of occurrences of each species across all examples of each habitat type. Significant differences between these frequencies were tested using Log-likelihood Ratio contingency table analysis (Zar 1984). Pearson's chi-square statistic was not used due to the high number of taxa absent from kettlehole and coastal peatland habitats.

Differences between the average size and richness of the three peatland types were analyzed using ANOVA. For richness, this analysis was also conducted on the subset of sites falling within the range of overlap in habitat size for the three peatland types (2.68–34.31 ha).

The relationship between species richness vs. natural log of habitat size for each of the habitats was analyzed using linear regression. Natural-log transformed habitat size was used as the independent variable in these models as it provided a better fit for the assumptions of linear regression than the untransformed data. The testing of differences between the best-fit slopes and intercepts for those habitats demonstrating a significant species-area relationship were determined by analyzing the significance of a binary variable (representing habitat type) which was added into the models (following methods outlined in Kleinbaum et al. 1988).

RESULTS

Size and distribution of peatland sites. A strong statistical difference ($p=0.007$; $r^2=0.136$) was observed in mean size of the three peatland types (Table 1). Average muskeg size was 300% greater than average coastal peatland size, which was 50% greater than average kettlehole peatland size.

Muskegs were found to be limited to the general vicinity of the divide basin (Figure 1). While occurring in all four counties, none were located in the pitted outwash plain extending from eastern Douglas to eastern Bayfield County. Kettlehole peatlands occurred in all four counties, but were most frequently encountered in the pitted outwash plain extending from Brule in Douglas County to Lake Owen in central Bayfield County. Coastal peatland sites were essentially limited to the Bayfield Peninsula, although three sites

Table 1. ANOVA of peatland size (in hectares) vs. peatland type.

Peatland Type	Min	Max	Mean	Standard Deviation
Muskeg	1.59	288.1	37.41	50.22
Kettlehole	0.49	67.24	6.98	14.36
Coastal	2.68	34.31	11.55	9.79

Summary of ANOVA analysis: $r^2=0.136$; $p=0.007$

were also encountered on Madeline Island. A number of additional coastal peatland sites occur in the Apostle Islands (Judziewicz and Koch 1993) and the Kakagon Slough, but were not sampled due to logistical and time constraints.

Butterfly faunas of peatland habitats. A total of ten peatland-obligate butterfly taxa were from muskeg sites (Table 2). The most frequent of these were *Incisalia augustinus* (recorded from 81% of surveyed sites), *Clossiana eunomia dawsonii* (43%), *Oeneis jutta* (41%), *Lycaena dorcas* (35%), and *Clossiana freija* (32%). Five peatland-obligate taxa were located from kettlehole sites. The most frequent of these were *Clossiana eunomia dawsonii* (recorded from 58% of surveyed sites), *Incisalia augustinus* (33%), and

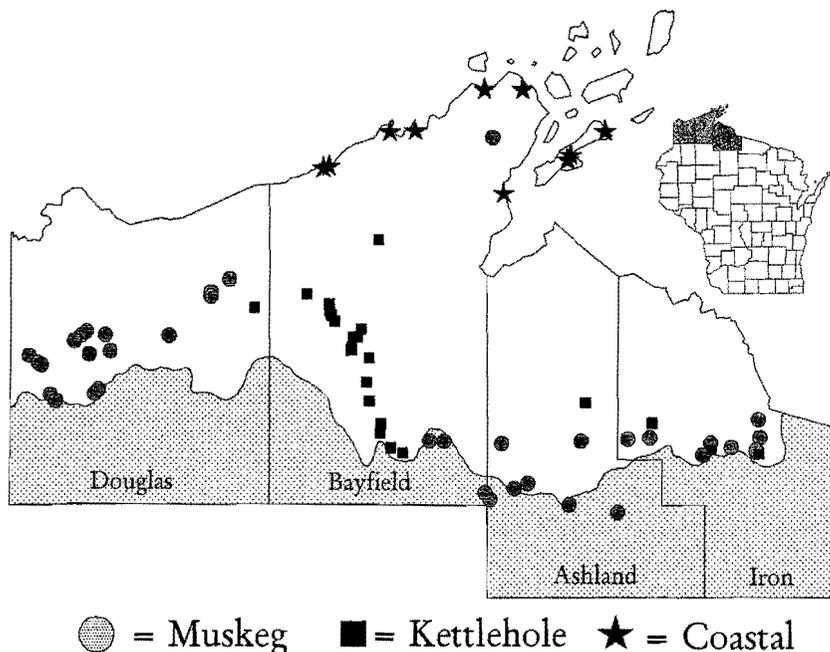


Figure 1. Location of the Lake Superior drainage basin in northwestern Wisconsin and of surveyed peatland sites.

Table 2. Absolute and relative occurrence frequency of peatland-obligate butterfly taxa among the three peatland types

Taxon	Peatland Type					
	Muskeg		Kettlehole		Coastal	
	Abs.	Rel.	Abs.	Rel.	Abs.	Rel.
<i>Incisalia augustinus</i>	30	81%	8	35%	1	10%
<i>Clossiana eunomia dawsonii</i>	16	43%	14	61%	4	40%
<i>Oeneis jutta</i>	15	41%	3	13%	0	
<i>Lycaena dorcas</i>	13	35%	0		0	
<i>Clossiana freija</i>	12	32%	0		0	
<i>Lycaena epixanthe</i>	7	19%	7	30%	9	90%
<i>Clossiana titania</i>	6	16%	0		0	
<i>Coenonympha inornata</i>	4	11%	1	4%	4	40%
<i>Clossiana frigga saga</i>	2	5%	0		0	
<i>Erebia discoidalis</i>	2	5%	0		0	
Total Sites Sampled	37		23		10	

Log-likelihood Ratio test statistic: 66.68

Degrees of freedom: 18

 $p < 0.00001$

Table 3. ANOVA of peatland-obligate butterfly richness per site as a function of peatland type.

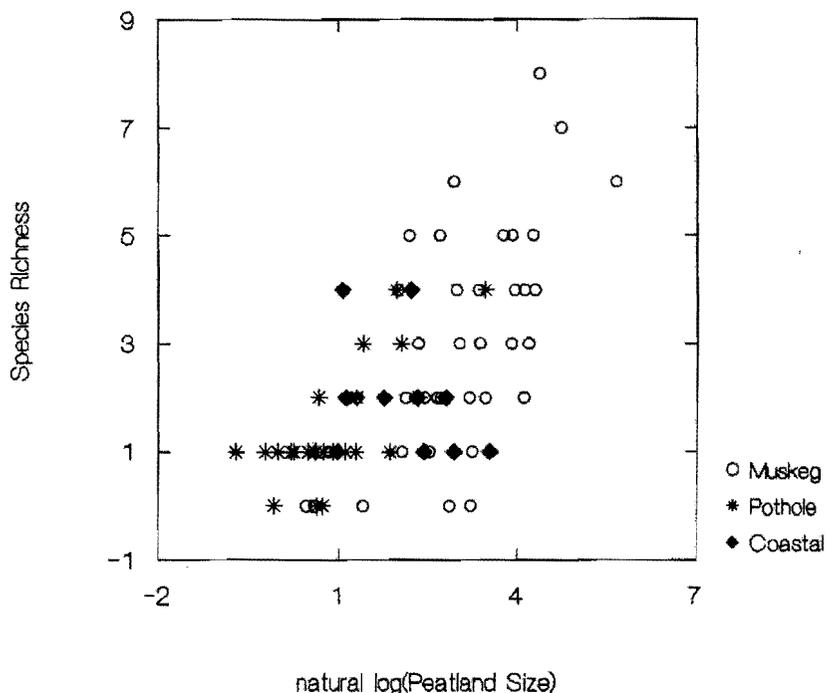
Peatland Type	All sites			Sites within range of habitat size overlap		
	n	Mean	Std. Dev.	n	Mean	Std. Dev.
Muskeg	37	3.00	2.07	22	2.46	1.68
Kettlehole	23	1.38	1.14	9	2.33	1.23
Coastal	10	2.00	1.16	10	2.00	1.16

Summary of ANOVA analysis for: All sites— $r^2 = .168$; $p = 0.002$ Sites within overlap range— $r^2 = .017$; $p = 0.725$

Lycaena epixanthe (29%). Four peatland-obligate taxa were located from coastal peatland sites. The most frequent of these were *Lycaena epixanthe* (recorded from 90% of surveyed sites), *Clossiana eunomia dawsonii* (40%), and *Coenonympha inornata* (40%). These differences in species frequency between peatland types proved to be highly statistically significant ($p < .00001$)

Species diversity patterns. Significant differences ($p < 0.002$; $r^2 = 0.168$) were observed in mean site richness of peatland-obligate species across the three peatland types (Table 3), with muskegs typically being the richest (3 taxa/site), followed by coastal (2 taxa/site), and kettlehole (1.38 taxa/site) sites. A strong relationship was also found between log-transformed habitat size and species richness in all but coastal peatland habitats (Figure 2; Table 4). Natural-log transformed habitat area was found to explain 41%, 52%, and 14% of the observed variation in peatland-restricted species richness of muskeg, kettlehole, and coastal peatland habitats, respectively.

When the ANOVA of richness by peatland type was recalculated using only those sites within the range of overlap in habitat size between all three



Peatland taxa distribution, ecology and behavior

LYCAENIDAE

Incisalia augustinus Westwood

This is the most frequent peatland-obligate butterfly in northwestern Wisconsin, being observed at 6 Ashland, 7 Bayfield, 17 Douglas, and 9 Iron county stations. While occurring in all peatland types, populations were most frequently encountered in muskegs, and almost completely avoided coastal sites. Individuals were often found roosting and nectaring on Heaths, particularly Leatherleaf.

Lycaena dorcas Kirby

This taxon was limited to 6 Ashland, 1 Bayfield, 3 Douglas, and 3 Iron County muskeg sites. No more than 5 individuals were noted at any site. Most adults were observed in relatively dry, open site centers. No oviposition or nectaring was observed. Shrubby Cinquefoil (*Potentilla fruticosa* L.), the host plant typically listed for this species (e.g., Newcomb 1910, Opler and Malikul 1992), does not occur on any of the observed stations, and is not known to occur within 150 km of the study region. While Laplante (1985) also lists Marsh Cinquefoil (*Potentilla palustris* (L.) Scop.) as a host for eastern Canadian populations, only once during field work were individuals observed flying in its vicinity. Strangely, no populations were found from coastal peatlands which supported the largest Marsh Cinquefoil populations. Use of some other unidentified larval host is likely in this region, possibly Cranberry (*Vaccinium oxycoccus* L.).

Lycaena epixanthe Boisduval & LeConte

This species was located at 5 Ashland, 11 Bayfield, 4 Douglas, and 3 Iron County peatlands. While occurring in all peatland types, populations were always restricted to wet, open *Sphagnum* mats with abundant Cranberry. Most muskeg and kettlehole populations were located on floating *Sphagnum* lawns immediately adjacent to bog lakes or next to roadsides where drainage had been impeded. In coastal peatlands it was restricted to *Sphagnum* islands within more eutrophic *Carex lasiocarpa* mats. At only one site were more than 25 individuals observed.

NYMPHALIDAE

Clossiana eunomia dawsoni (Barnes & McDunnough)

This taxon was located at 17 Bayfield, 15 Douglas, and 2 Iron County peatlands. Populations were observed from all peatland types. Although frequent in the western section of the study region, it was not observed on seemingly appropriate sites ranging from eastern Bayfield to central Iron County. Fewer than 5 individuals were noted at most stations. Individuals were largely seen on very wet *Sphagnum* islands or floating mats supporting a dense growth of Cranberry and Pitcherplant (*Sarracenia purpurea* L.). Oviposition on Cranberry was observed in 1995 in northeastern Wisconsin.

Cranberry has been identified as the larval host for eastern Canadian populations (Laplante 1985). Adults were frequently seen at site margins nectaring on Labrador Tea (*Ledum groenlandicum* Oeder.).

Clossiana freija (Thunberg)

This species was limited to 9 Douglas and 3 Iron County muskeg sites. Individuals were most frequently observed in dry Heath—*Carex oligosperma* openings, usually near site centers. These observations counter Opler and Krizek (1984) who state this species prefers bog margins. Individuals rapidly flew at or just above the cover of dead, matted Sedge leaves. Favored roosting sites appeared to be low, Sphagnous areas which were protected from the wind by the previous year's dead Sedge growth. In June of 1997 oviposition was noted on Cranberry in northeastern Wisconsin.

Clossiana frigga saga (Staudinger)

This taxon was only observed on single muskeg sites in Douglas and Ashland counties. Both were large and supported colonies of Bog Birch (*Betula pumila* L.) and Bog Willow (*Salix pedicellaris* Pursh.). Adults had an extremely rapid flight, and roosted on various low shrubs. Although Bog Birch has been listed as the host plant in northern Michigan (Opler and Krizek 1984), adults exhibited a much stronger association with Bog Willow, and were always limited to its immediate vicinity. Shrub willows have been noted as the host for *C. frigga saga* in Alberta (Opler and Krizek 1984).

Clossiana titania (Esper)

This species was limited to 6 muskeg sites in western Douglas County. All of these had extensive dry Heath—*Carex oligosperma* openings supporting *Clossiana freija* populations. Adults were only rarely seen within sites, however, and were most often observed nectaring and mating up to ½-mile from sites along upland openings and roadsides. Roadsides may serve as migration corridors, as individuals frequently patrolled these habitats. Oviposition plants and larval hosts have not yet been noted.

SATYRIDAE

Coenonympha inornata Edwards

This species was observed at 1 Ashland, 5 Bayfield, and 3 Douglas county peatland sites. It has also been located from at least 10 additional upland stations in the study region, including old fields and sand barrens. Peatlands harboring this species all possessed large, Sedge-dominated openings. Individuals were often scattered and rare within sites. Nectaring and oviposition were not noted for any of these populations.

Erebia discoidalis (Kirby)

This species was only located from single muskeg sites in Ashland and Douglas counties, with only single individuals being noted at each site. Both

locations have extensive *Carex oligosperma* and *Eriophorum spissum* meadows. Individuals from this region, as well as those from northeastern Wisconsin, appear to most frequently patrol the margins of these openings. Oviposition and nectaring has not been observed.

Oeneis jutta (Hübner)

This species was observed from 4 Ashland, 4 Bayfield, 8 Douglas, and 2 Iron county peatland sites. Populations were most frequently encountered in muskegs, but were absent from coastal sites. Kettlehole populations were limited to sites possessing well developed Black Spruce groves. Rarely were more than 10 individuals observed within a single site. Contrary to Masters and Sorenson (1969), individuals did not favor bog edges, but were rather encountered throughout sites in Black Spruce groves adjacent to *Eriophorum spissum* openings. Individuals roosted on small Spruce branches with wings folded and were well camouflaged. When flushed, their flight was rapid and quick, and usually limited to the extent of the nearest opening. Nectaring was observed on Labrador Tea. Oviposition has not been witnessed.

DISCUSSION

Faunas of the three peatland types. Muskeg sites physically differed from other peatlands in their larger size, and their drier and presumably more nutrient poor soils. The wettest microsites on these habitats were limited to moats at site margins and to floating mats at the edge of bog lakes. Five taxa (*Clossiana freija*, *Clossiana frigga saga*, *Clossiana titania*, *Erebia discoidalis*, *Lycaena dorcas*) were restricted to muskegs. Two of these (*Clossiana freija*, *Lycaena dorcas*) were among the more frequently encountered muskeg taxa. The number of taxa observed per site was significantly greater than in other peatland types. This difference is apparently related to the larger average size of muskegs, as no significant differences were observed in richness when habitat size was limited to the range of overlap between the three peatland types. This conclusion is also supported by the statistically similar species-area relationships found between muskeg and kettlehole sites. However, the relationship between site area and species richness is undoubtedly related to more than simple area-sensitivity of the species concerned. As all species which are limited to muskegs are restricted to dry Heath-Sedge meadows, the lack of this microhabitat from smaller peatlands, rather than habitat size, *per se*, may be the actual factor limiting their occurrence.

Kettlehole sites were generally smaller and wetter than muskegs. Plant communities varied greatly between sites, ranging from acid Leatherleaf mats to inundated Sedge meadows and floating *Sphagnum* lawns. No taxa were restricted to this peatland type. While the two most frequent taxa are shared between kettleholes and muskegs (*Clossiana eunomia dawsonii*, *Incisalia augustinus*), the third most frequent kettlehole taxon (*Lycaena epixanthe*) was only the sixth most frequent muskeg taxon. Species richness of kettlehole sites was half that observed from muskegs.

Coastal peatlands were typically dominated by open tamarack groves and opening meadows of *Carex lasiocarpa* and *Carex lacustris* Willd. These sites also harbored a number of relative calciphiles such as *Triglochin maritima* L., *Salix candida* Flüggé, and *Scirpus hudsonianus* (Michx.) Fern. *Sphagnum*-dominated islands or ridges set above the Sedge turf were the

only microhabitats within coastal sites which supported acidophilic plants (like Cranberry) and peatland-obligate butterfly populations. The dominant obligate butterfly of coastal peatlands (*Lycaena epixanthe*) was much less frequent in the other habitats. However, coastal peatlands harbored the fewest total taxa, and had the fewest average taxa per site of all peatland types sampled. Additionally, coastal peatlands were the only type to not demonstrate a significant species-area relationship.

Within-site distribution of peatland taxa. Most published reports on the within-site distribution of the surveyed taxa (e.g., Masters and Sorenson 1969, Masters 1971a, 1971b, Opler and Krizek 1984) suggest that peatland margins are preferred by adults. This was not found to be the case during this study.

In muskegs, *Coenonympha inornata*, *Clossiana freija*, *Erebia discoidalis*, *Incisalia augustinus* and *Lycaena dorcas* adults were most often found in open *Carex oligosperma* meadows in site centers. *Clossiana frigga saga* was always found in proximity to its host plant, Bog Willow, which can occur from the center to margin of sites. *Oeneis jutta* was usually found flying within or at the periphery of Black Spruce groves throughout sites. Although apparently requiring *Carex oligosperma* meadows for larval life stages, adult *Clossiana titania* were mostly found adjacent to sites in upland borders possessing abundant nectar sources. Only *Clossiana eunomia dawsonii* and *Lycaena epixanthe* were reliably encountered at site margins, as their preferred habitat (floating *Sphagnum* mats) develop on moats. However, these two species were also commonly found on floating mats surrounding lakes in site centers.

In kettleholes, peatland butterflies (particularly *Clossiana eunomia dawsonii* and *Lycaena epixanthe*) favored *Sphagnum* lawns surrounding or islands within central lakes. *Oeneis jutta* adults were observed flying only in proximity of Black Spruce groves, which were limited to dry areas within the largest sites.

In coastal sites, all peatland taxa were restricted to isolated *Sphagnum* ridges and islands. The lack of correlation between area covered by this microhabitat vs. total site size (some large sites possess fewer *Sphagnum* patches than are present in smaller sites) may help explain the lack of observed relationship between species richness and total habitat size in this peatland type. A more accurate assessment of species-area relationships in coastal peatlands will probably require estimation of area covered by *Sphagnum* islands within each site.

Biogeographic relationships of the peatland faunas. Four of the peatland taxa (*Clossiana eunomia dawsonii*, *Coenonympha inornata*, *Incisalia augustinus*, and *Lycaena epixanthe*) were common to all peatland types. These taxa have boreal, western, and northeastern ranges respectively (Scott 1986). *Oeneis jutta*, found in both muskeg and kettlehole peatland sites, also has a boreal range (Scott 1986). The remaining five taxa (*Clossiana freija*, *Clossiana frigga saga*, *Clossiana titania*, *Erebia discoidalis*, *Lycaena dorcas*), all restricted to muskeg sites, range to northern Alaska and the high arctic islands of Canada (Scott 1986). All five of these species appear to favor dry, open Sedge-Heath meadows, which often constitute a large proportion of muskeg sites. The limitation of these arctic-boreal species to this microhabitat may indicate that muskeg Sedge-Heath meadows, from a lepidopteran point of view, may represent the closest analogue to tundra and taiga environments in northern Wisconsin.

From these analyses it is clear that all peatland areas in northwestern Wisconsin are not equal in relation to their butterfly faunas. Muskeg peatlands possess a significantly different fauna from kettlehole and coastal sites, and harbor twice the total number of taxa, as well as up to three times

the number of taxa per site as compared to the remaining peatland types. The muskeg fauna is also significantly enriched in arctic-boreal taxa. These results suggest that a multiplicity of peatland ecosystems in Wisconsin should be recognized to help us better characterize the biological diversity of these sites.

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