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Jutta Arctic (*Oeneis jutta*) (Lepidoptera: Nymphalidae) Populations in Central and Northern Wisconsin: Localized Butterfly Populations in a Naturally Fragmented Landscape

Scott R. Swengel^{1*}, Ann B. Swengel¹

Abstract

We recorded *Oeneis jutta* (Hübner) (Lepidoptera: Nymphalidae) at 60 of 78 peatland sites in central and northern Wisconsin on butterfly transect surveys on 113 dates during 2002–11. Additional observations come from informal observations on 19 dates in 12 years during 1987–2001. Most sites where we did not find *O. jutta* had little survey effort. The areas with the lowest *O. jutta* abundance (coastal and inland Bayfield County) had the shortest flight periods recorded in this study. *O. jutta* abundance negatively and significantly correlated with increasing wind speed and later times of day. *O. jutta* abundance significantly varied by bog vegetation type and in similar bog vegetation between subregions. Within each bog type, *O. jutta* significantly increased in abundance with greater tree cover. *O. jutta* occurred in the full range of bog sizes surveyed (1.84–114.80 ha), including the most isolated small peatlands. *O. jutta* showed virtually no tendency to venture out of bogs. It was rarely found in roadsides (only when they bisected an occupied peatland) and not farther away from a peatland. *O. jutta* was significantly more abundant in even than odd years in northeast Wisconsin but not in the other subregions. Wisconsin peatlands present a natural experiment showing that localized butterfly populations such as *O. jutta* can persist for long periods in isolated sites as long as they remain relatively stable vegetatively.

A major threat to biodiversity is human-caused habitat loss, with fragmentation and degradation of extant patches (Brown 1997, van Swaay et al. 2006, Forister et al. 2010). Butterfly populations fare more poorly in isolated or small sites, with nearer and larger sites more likely to remain occupied or be re-colonized (Bulman et al. 2007, Hanski and Pöyry 2007, Dover and Settele 2009). Both habitat quality and landscape configuration are important for maintaining butterfly populations (Dennis and Eales 1997, Thomas et al. 2001, Hanski and Pöyry 2007, Dennis 2010), and both are under threat in a human-degraded, fragmented landscape. As a result, much research in conservation biology concerns how to counteract the effects of habitat loss and fragmentation on vulnerable species (e.g., Mattoni et al. 2001, Thomas et al. 2001, Dennis and Hardy 2007, Swengel and Swengel 2007, Dover and Settele 2009, Dennis 2010, Dover et al. 2011).

In temperate areas of North America, bog (peatland) vegetation is naturally isolated and forms a low proportion of the natural landscape. Bogs are well known for the long-term stability of their flora and insect faunas (Spitzer et al. 1999, Spitzer and Danks 2006, Whitehouse 2006, Whitehouse et al. 2008). In Wisconsin, peatlands occur primarily in central and northern areas (Curtis

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1959). Prior to European settlement, peatlands occurred in < 1% of the Wisconsin landscape (even counting only the northern third of the state) (Hoffman 2002). Most of that vegetation is still extant, with only 9% loss, more being lost in central than northern Wisconsin. Much of what is left, especially in northern Wisconsin, is relatively undegraded. Primary human impacts are roads, ditches, and logging along the margins; conversion to cranberry agriculture and peat harvesting have occurred more in central Wisconsin bogs (Curtis 1959).

As a result, bogs present the opportunity to learn how localized butterfly populations function in relatively undisturbed sites in a naturally fragmented landscape. Nekola (1998) conducted a systematic survey of northwestern Wisconsin peatlands and their associated butterflies in 1996. In this paper, we analyze our Wisconsin bog butterfly surveys to extend Nekola's (1998) study and our prior analyses (Swengel and Swengel 2010, 2011) that describe patterns of bog butterfly population occurrence. This study focuses on one bog-specialist butterfly, Jutta Arctic (*Oeneis jutta* (Hübner)). We analyze our survey results in relation to weather factors, vegetative characteristics, geography, and patch size. These results should be useful for designing and interpreting survey protocols and understanding butterfly populations in fragmented landscapes.

Methods

Study Regions. The primary study region contains 75 bog sites scattered across an area 367 km east-west by 169 km north-south (45.33° -46.86°N, 88.21° -92.56°W) in 14 contiguous counties spanning the entire breadth of northern Wisconsin (Table 1). At 14 of these sites, we also surveyed the lowland (wetland) roadside ditch through/adjacent to the bog or the upland roadside corridor 20–350 m from the bog. In central Wisconsin, the three bogs we surveyed in two contiguous counties (Jackson, Wood) are in an area 29 km east-west by 4 km north-south (44.31° -44.34° N, 90.19° -90.56°W), which is 169 km south of the nearest study site in the northern study region. Nekola's (1998) study region comprised sites in and adjacent to the Lake Superior drainage basin in four contiguous counties (Ashland, Bayfield, Douglas, Iron) bordering the south lakeshore. This area is the north part of the west half of our northern study region. Most of our sites in those counties fall within his study region. We biased toward high-quality examples of peatland vegetation open to public visitation and efficient to access and travel between. Nonetheless, peatlands often present difficulties of access to and across them, which reduces survey efficiency. Roadside survey areas were selected because we noticed bog butterflies using them; these areas were en route to or from a bog study site or they appeared potentially interesting for either bog or other butterfly species.

Nekola (1998) described three peatland types: muskeg (black spruce *Picea mariana*-cottongrass *Eriophorum spissum*-wiregrass *Carex oligosperma*-*Sphagnum* savanna similar in elevation to surrounding uplands), kettlehole (*Sphagnum*-leatherleaf *Chamaedaphne calyculata* mats, often floating on lakes or sunk in depressions much lower than the surrounding landscape), and coastal peatland (tamarack *Larix laricina*-sedge, especially *Carex lasiocarpa*, mats with ridges of muskeg-like vegetation in estuaries along the Lake Superior coast). Many aspects of the flora are similar among these three types (Nekola and Kraft 2002), echoing Curtis's (1959) description of remarkably uniform bog structure and composition throughout the circumboreal region. Nekola's (1998) kettleholes correspond to Johnson's (2011) poor fen, and Nekola's muskegs to Johnson's (2011) "acid peatlands." Nekola (1996) identified coastal peatlands as intermediate fens. We focused our surveying there on areas most resembling acid peatlands. Based on Johnson's (2011) peatland classification, we did not survey rich peatlands (rich fens), where northern white cedar *Thuja occidentalis* is a prominent indicator. Our study sites fit his category of "acid peatland," which includes both poor fens and bogs (the most nutrient-poor peatland).

Table 1. Summary statistics on all surveys in Wisconsin peatlands during *O. jutta* flight period during 2002–11.

	N surveys	N <i>O. jutta</i> recorded	Total km	Total hours	<i>O. jutta</i> per hour	Total sites	N sites no detection
Northern Wisconsin Peatlands							
Coastal Bayfield Co. ¹	50	8	29.53	11.63	0.69	7	4
Inland Bayfield Co. ²	70	19	39.35	15.20	1.25	8	1
Northeast ³	297	408	121.62	44.10	9.25	20	6
North central ⁴	421	249	175.92	68.43	3.64	23	5
Northwest ⁵	292	401	173.08	69.03	5.81	17	2
Roadsides ⁶	47	2	15.53	5.56	0.36	14	12
Central Wisconsin ⁷	14	21	7.64	2.95	7.12	3	0
Total	1191	1108	562.67	216.90	5.11	78	18

¹Coastal peatlands only²Kettleholes only³Florence, Forest, Marinette, Oconto, eastern Oneida counties⁴Ashland, Iron, Lincoln, Price, eastern Sawyer counties⁵Bayfield, Burnett, Douglas, Washburn counties⁶All roadsides were next to bog study sites, and so do not add to the total number of study sites.⁷Jackson, Wood counties

Surveys. We conducted formal transect surveys throughout *O. jutta* flight period on 113 dates during 2002–11 (Table 1). We surveyed in a rotation through the western, central, and eastern sections of the northern study region, starting before and continuing after *O. jutta* flight period each year. We tried to cover one section per weekend, or more if a section was missed the previous weekend and/or if time allowed. But we missed an occasional weekend due to weather or another commitment. We also had visited peatlands informally in both study regions on 19 dates in 12 years during 1987–2001 in *O. jutta* flight period but had not yet standardized a route or recorded weather and time and distance spent surveying.

We walked transect surveys along a similar route per visit to a site at a slow pace (about 2–3 km/hr) on parallel routes 5–10 m apart (Swengel and Swengel 2010, 2011). We counted all adult butterflies observed ahead and to the sides, to the limit an individual could be identified, possibly with binoculars after being found and tracked. A new sampling unit was designated whenever the vegetation along the route varied markedly, in peatlands primarily based on estimated macrosite tree canopy (open bog < 10%, open savanna 10–24%, closed savanna 25–49%, forest opening 50–75% but we avoided canopy > 50% in our site and route selection). Temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying were recorded separately for each unit. Surveys occurred during a wide range of times of day and weather, occasionally in light drizzle so long as butterfly activity was apparent but not in continuous rain. We experienced severe constraints on obtaining suitable weather especially in spring. The negative effect of subpar weather on butterfly observation in our survey results is not a systematic bias, as we did not (and could not) bias which sites were surveyed in better weather. Thus, this factor confounds statistical power but doesn't systematically misdirect it. In the case of large-scale, long-term datasets, variation due to weather and time of day may be assumed to be random, so that their effects reduce precision or power of results but may not introduce bias (van Swaay et al. 2008).

Analyses. As in Nekola and Kraft (2002), we identified the flight period per year by the first and last date we observed *O. jutta* across each region. However, for purposes of identifying surveys with valid counts of zero for analysis, we excluded *O. jutta* absences during the period extending from the main flight period to the occasional one or two outlier individuals recorded days before or after all other individuals that year. Our population index is the peak survey count per site per brood, standardized to survey time, to create an observation rate (relative abundance) per hour per unit survey, to make results comparable among units of varying length. We did not set a standardized distance or time sampled per unit or per site because of the several orders of magnitude variation in size among sites. A standardized amount of sampling per site would either under-sample large sites or eliminate small sites from the study.

We used Nekola's (1996) peatland sizes and classifications for his study sites listed in Epstein et al. (1997). All kettleholes in this study were in the northwest subregion in inland Bayfield County and all coastal peatlands in coastal Bayfield County. Outside Nekola's study region, we classified some bogs as muskegs that clearly fit his definition. As Johnson (2011) described, peatland classification is a continuum defying distinct categories, especially since different parts of the same site may ally with different categories. However, all sites where we recorded *O. jutta* fit Johnson's (2011) concept of "acid peatland." As a result, sites not classified by Nekola's (1998) scheme are called "acid peatland" here. We estimated peatland size at three small sites by pacing out these obviously discrete patches. It was beyond our scope to estimate the size of the remaining sites outside Nekola's (1998) study area because we did not survey the entire peatland. It was beyond the scope of our survey dataset to calculate detection probabilities, which requires frequent re-samplings every few days at the same sites within brood, e.g., 6–8 times in Bried and Pellet (2012) and

Bried et al. (2012). As a result, we were not able to distinguish between false negatives (none found but species present) and true negatives (species absent on that date). Instead, we chose to analyze *O. jutta* abundance only in sites where we had ever recorded the species during our formal surveys. Our analyses are intended to describe distribution and abundance within occupied sites. An observation rate of 0 signifies either an abundance too low to be observed by us that day or true absence, and we did not attempt to distinguish between the two.

Analyses were done with ABstat 7.20 software (1994 Anderson-Bell Corp., Parker, Colorado). Statistical significance was set at two-tailed $P < 0.05$. Since significant results occurred at a frequency well above that expected due to spurious Type I statistical error, the critical P value was not lowered further, as more Type II errors (biologically meaningful patterns lacking statistical significance) would be created than Type I errors eliminated. All statistical tests in this study are non-parametric, because they do not require data to be distributed normally. All correlations were done with the Spearman rank correlation. To test for significant differences between matched pairs, we used the Wilcoxon signed ranks test and among unequal samples, the Mann-Whitney U test.

Results

Incidence. We recorded *O. jutta* at 60 of 78 sites on formal surveys during 2002–11 (Table 1). Most (14/18) of the sites where we did not record *O. jutta* were visited only 1–3 times in the entire study during the species' flight period.

The earliest date of *O. jutta* observation tended to become earlier the farther south the subregion (Table 2), from coastal Bayfield County to central Wisconsin. However, within the northern region, the northwest sites are a bit farther north than northeast, yet the earliest date in northwest was one week earlier than in northeast. The kettleholes and coastal peatlands of Bayfield County had the lowest observation rates per hour in peatlands (Table 1), and this corresponded to the shortest observed flight periods (Table 2). In northern Wisconsin, the latest observation date corresponds more to length of flight period, rather than how late the earliest date was (Table 1). The longest flight span occurred in northwest Wisconsin while flight spans were similarly intermediate in north central and northeast Wisconsin (Table 1). The number of days per year in the observed flight period was analyzable in the three northern Wisconsin subregions that had the most survey effort (Table 3 compared to Table 1). These flight period spans varied not just among years within subregion but also among subregions (Table 3). However, length of flight period across the entire northern region and within the three subregions did not relate to number of individuals found that year (Table 3) or to the regional abundance in Table 1. The range of variation in start, peak, and end of flight period across northern Wisconsin varied by over three weeks among years (Table 4).

Oeneis jutta abundance was negatively and significantly correlated with increasing wind speed and later times of day across the entire study (Table 5). When controlling for habitat preference, only the negative relationship to wind speed remained significant (Table 5).

Habitat associations. *O. jutta* abundance was significantly higher in muskegs and similarly lower in kettleholes and coastal peatlands (Table 6). Unclassified acid peatlands had an intermediate abundance that statistically associated with the low abundance sites. Within kettleholes and coastal peatlands, sites varied greatly in frequency of *O. jutta* observation (Table 7). However, we recorded the species in the most isolated sites surveyed (Valhalla at 2.83 ha and Pine Lake at 1.96 ha, > 7 and > 14 km from the nearest known peatland, respectively). Within each bog type, *O. jutta* consistently and significantly increased in abundance with increasing tree cover (Table 8, 9). The two peatlands we surveyed the most times yet still found no *O. jutta* were coastal peatlands

Table 2. Earliest and latest dates of *O. jutta* observations and N days in these flight periods during entire study (formal surveys and informal visits).

Subregion	Earliest date	Latest date	N days	Years visited
Northern Wisconsin				
Coastal Bayfield Co. peatlands	29 May	24 Jun	27	03–11
Interior Bayfield Co. kettleholes	21 May	24 Jun	35	88–11
Northeast	16 May	4 Jul	50	88–11
North central	15 May	28 Jun	45	87–11
Northwest	9 May	10 Jul	63	98–11
Central Wisconsin	2 May	15 Jun	45	97–11

Table 3. N days in observed *O. jutta* flight period each year during 2002–11 (N = 10 years), and Spearman rank correlation coefficients (*r*) (none significant) of flight period length and N individuals recorded per year.

	mean ¹	median	range	<i>r</i>
All northern Wisconsin	35.5	39.0	21–44	+0.085
North central	21.4	23.0	7–31	+0.340
Northwest	30.5	29.0	8–44	+0.122
Northeast	15.5	15.5	1–34	-0.086

¹In pairwise Wilcoxon signed ranks tests of flight period length per year among the three subregions, only northeast and northwest were significantly different (two-tailed $P = 0.02$).

Table 4. Variation in *O. jutta* start, peak, and end date in northern Wisconsin among years during 2002–11 (N = 10 years).

	mean	median	range ¹	span
Start date	24 May	26 May	9 May–2 Jun	25
Peak date	11 Jun	15 Jun	28 May–19 Jun	23
Northeast	13 Jun	14 Jun	1 Jun–27 Jun	27
North central	6 Jun	9 Jun	25 May–15 Jun	22
Northwest	10 Jun	12 Jun	26 May–20 Jun	26
End date	28 Jun	1 Jul	18 Jun–10 Jul	23

¹In pairwise Wilcoxon signed ranks tests of peak date per year among the three subregions, only northeast and north central were significantly different (two-tailed $P = 0.008$).

Table 5. Spearman rank correlation coefficients (r) of *O. jutta* abundance (individuals/hr per unit survey) on peak survey per site per year during 2002–11 with weather factors and surveying timing, for all sites and for muskegs with more canopy than openest category (see Table 6, 8). Only surveys at sites where we recorded *O. jutta* are included for analysis.

	All bogs			Non-open muskegs		
	N	r	P	N	r	P
Cloud cover	631	-0.052	NS	280	-0.072	NS
Percent sunshine	631	+0.019	NS	280	+0.065	NS
Temperature	631	-0.066	NS	280	-0.076	NS
Wind speed	631	-0.157	< 0.01	280	-0.136	< 0.05
Time of day	631	-0.104	< 0.01	280	-0.030	NS
Crepuscularity	631	+0.018	NS	280	+0.039	NS

Table 6. Mean \pm SD, median, and range of *O. jutta* abundance (individuals/hr) by bog type on peak surveys limited to *O. jutta* sites in northern Wisconsin during 2002–11. Bog types not sharing any letters have statistically different abundances (Mann-Whitney U test two-tailed $P < 0.05$).

Bog type	N	mean		SD	median	range
Muskeg	367	10.19	A	15.85	4.80	0–127.50
Kettlehole	42	1.66	B	2.97	0.00	0–10.91
Coastal peatland	18	2.10	B	2.54	0.00	0–6.32
Unclassified acid peatland	208	4.50	B	7.85	0.00	0–51.06

Table 7. Observations of *O. jutta* in inland Bayfield kettleholes (K) and coastal Bayfield peatlands (C), expressed as proportion of years found and proportion of surveys found, and as mean individuals/hr on peak survey each year, in *O. jutta* flight period during 2003–11 (no such sites were surveyed in 2002).

	Years found/ Years surveyed		Times found/ Times surveyed		Mean abundance
K East Crane Lake	6/7	86%	7/9	78%	5.04
C Port Wing Bibon Lake	6/9	67%	6/11	55%	3.90
K Valhalla	1/3	33%	1/6	17%	1.48
K East Wishbone Lake	2/8	25%	2/14	14%	0.45
K Pine Lake	1/6	17%	1/10	10%	0.71
K East Roger Lake	1/7	14%	1/12	8%	0.51
C Port Wing Boreal Forest West	1/8	13%	1/10	10%	0.31
C Bark Bay	0/8	0%	0/10	0%	0.00
C Lost Creek	0/6	0%	0/10	0%	0.00

Table 8. Mean \pm SD, median, and range of *O. jutta* abundance (individuals/hr) by bog structure (coded by category of canopy, with intermediate values) on peak surveys in northern Wisconsin during 2002–11. Only sites where we recorded *O. jutta* are included for analysis.

Canopy code	N	mean	SD	median	range
1 - open	145	2.39	5.75	0.00	0–51.43
1.5	17	9.20	10.69	6.32	0–45.71
2 - open savanna	283	6.62	11.35	0.00	0–80.84
2.5	68	10.60	15.99	5.49	0–81.88
3 - closed savanna	113	14.74	19.00	9.80	0–127.50
4 - open forest	1	20.00			

Table 9. Spearman rank correlation coefficients (r) of *O. jutta* abundance (individuals/hr) on peak unit surveys per site per year for all sites and by bog type in northern Wisconsin during 2002–11 with estimated percent tree canopy. Only sites where we recorded *O. jutta* are included for analysis.

	N	r	P	canopy mean	canopy range
All bogs	612	+0.411	< 0.001	11.7	1–50
Muskeg	358	+0.389	< 0.001	12.2	1–50
Kettlehole	42	+0.557	< 0.001	12.1	3–30
Coastal peatland	18	+0.718	< 0.01	6.5	5–8
Unclassified acid peatland	185	+0.407	< 0.001	10.6	0–30

(Table 7) where we did not survey the most likely habitat for *O. jutta* (the most canopied areas) due to access difficulties. When the sample was limited to the bog type (muskeg) and canopy structure (not open) that *O. jutta* favored (Table 10), this species was significantly more abundant in northwest than north central. In northeast Wisconsin, *O. jutta* abundance exhibited extreme variation as evident in the SD and maximum observation rate, but the median was intermediate between the other two analyzed subregions and related statistically to both regions (Table 10).

We found two *O. jutta* in roadside surveys (Table 1). These occurred at two of the sites where the road bisected a muskeg in which we also recorded *O. jutta*. Thus, peatland vegetation came into the ditches on each side of the road. In surveys of nearby upland roadsides, we found no *O. jutta* but did find numerous other butterflies, most frequently *Phyciodes selenis* (Kirby), *Carterocephalus palaemon* (Pallas), and *Poanes hobomok* (Harris). At sites where we walked through more upland forest to a bog where we found *O. jutta*, we found no *O. jutta* on those access walks. However, we did note other butterflies in these upland forests, including other members of the same subfamily (Satyriinae) as *O. jutta*: *Enodia anthedon* Clark, *Satyroides appalachia* (Chermock), and *Megisto cymela* (Cramer). We also encountered no *O. jutta* on extensive surveys of upland barrens in northern Wisconsin in the same counties as these bog study sites (Swengel and Swengel 2010), including barrens within 100 m of bogs. By contrast, two bog specialist butterfly species were relatively over-represented in boggy roadsides compared to off-road peatland vegetation, and a few individuals occurred in nearby upland roadsides, although still highly under-represented there (Swengel and Swengel 2011).

Table 10. Mean \pm SD, median, and range of *O. jutta* abundance (individuals/hr) in muskegs with more canopy than openest canopy code (open) in Table 8, by subregion on peak surveys in northern Wisconsin during 2002–11. Means not sharing a letter are significantly different (Mann-Whitney *U* test $P < 0.05$).

Subregion	N	mean		SD	median	range
Northeast	76	18.64	AB	25.46	7.02	0–127.5
North Central	106	8.80	B	11.02	5.52	0–48.0
Northwest	96	11.86	A	11.19	9.60	0–49.4

We saw *O. jutta* in the full range of bog sizes surveyed (1.84–114.80 ha), although some of the surveyed bogs with missing values for site size in this study may be larger than that (e.g., Price County). The overlap in bog size among the three peatland types was fairly narrow (Table 11). In that small sample of surveys, *O. jutta* abundance and tree canopy were significantly higher in muskegs than kettleholes and coastal peatlands. In the muskegs, *O. jutta* abundance correlated significantly and negatively with bog size, but percent tree canopy also had a significant negative relationship to bog size (Table 12). In the kettleholes, which were smaller on average and varied much less in size, both *O. jutta* abundance and tree canopy covaried significantly with bog size (Table 12).

Surveys in more canopied areas had significantly lower wind, but other weather and time of day variables showed no pattern relative to canopy (Table 13). Within a canopy classification, however, *O. jutta* abundance did not correlate significantly with wind, although all correlations were negative (Table 14). Within bog type, *O. jutta* abundance correlated significantly (negatively) with wind only in muskegs (Table 15). However, in all bog types, wind speed correlated more strongly with tree canopy than with *O. jutta* abundance. This relationship was negative except in coastal peatlands. However, only two sites were in that sample, and the site with the lower canopy on our surveys actually had more surrounding forest that blocked wind more effectively than at the other site.

Annual Variation. *O. jutta* was dramatically more abundant in odd than even years in northeast Wisconsin, with average abundance 19 times as high in odd years as even (Fig. 1). This difference in abundance between even and odd years was significant in northeast but not in the other two subregions (Table 16), where abundances averaged a bit higher in even years than odd. The low abundances in the coastal peatlands were a bit higher in odd years than even, and fairly similar between even and odd years in the kettleholes (Fig. 2, Table 16). The one site in central Wisconsin showed fluctuation among years (Fig. 2) but a bit higher abundance in even than odd years (Table 16). Weather and time of day did not vary significantly between even and odd years on the surveys at long-term sites in northeast Wisconsin, except for temperature (in favor of even years) and wind, in favor of odd years (Table 17).

Discussion

Incidence. We found *O. jutta* at most (77%) peatland study sites (Table 1), and most sites where we did not find it had little survey effort. The areas with the lowest observation rates (coastal and inland Bayfield County: Table 1) had the shortest overall flight periods recorded in this study (Table 2). The other subregions had flight spans similar to or greater than the 46 days (20 May to 4 July) reported for the Upper Peninsula of Michigan (Nielsen 1999, Perkins 2007).

Table 11. Mean \pm SD, median, and range of *O. jutta* abundance (individuals/hr) by bog type on peak surveys limited to *O. jutta* sites ranging in size from 2.83 to 16.56 ha in northern Wisconsin during 2002–2011. Bog types not sharing any letters have statistically different abundances (Mann-Whitney *U* test two-tailed $P < 0.05$).

	N unit surveys	<i>O. jutta</i> individuals/hour			Mean % canopy	N sites	Size mean	Size range	
		mean	SD	median					range
Muskeg	23	14.28 A	18.42	10.00	0–91.20	20.43 A	3	8.91	2.83–14.95
Kettlehole	29	2.14 B	3.36	0.00	0–10.91	15.62 B	3	6.54	4.12–7.82
Coastal	18	2.10 B	2.54	0.00	0–6.32	6.50 C	2	9.70	2.83–16.56

Table 12. Spearman rank correlation coefficients (*r*) of bog size (ha) with *O. jutta*/hr and with percent tree canopy in muskegs and kettleholes. Only surveys at sites where we recorded *O. jutta* are included for analysis. The sample for coastal peatlands was too small for this analysis.

Bog type	<i>O. jutta</i> /hr		% tree canopy		Bog size	
	N	<i>r</i>	N	<i>r</i>	mean	range
Muskeg	195	-0.192	190	-0.322	71.89	2.83–114.80
Kettlehole	42	+0.492	42	+0.824	4.57	1.84–7.82

Table 13. Spearman rank correlation coefficients (r) of percent tree canopy with weather and time of day variables on peak unit surveys ($N = 603$) per site per year during 2002–2011 in northern Wisconsin. Only sites where we recorded *O. jutta* are included for analysis.

	r	P
Cloud cover	-0.060	NS
Percent sunshine	+0.029	NS
Temperature	-0.030	NS
Wind Speed	-0.340	< 0.01
Time of day	-0.036	NS
Crepuscularity	+0.078	~0.10

Table 14. Spearman rank correlation coefficients (r) (none significant) of *O. jutta* abundance (individuals/hr) on peak unit surveys ($N = 603$) per site per year during 2002–2011 with wind speed, by bog structure (category of canopy) as in Table 8. Only sites in northern Wisconsin where we recorded *O. jutta* are included for analysis.

	N	r
1 - open	145	-0.108
1.5	17	-0.414
2 - open savanna	281	-0.012
2.5	61	-0.173
3 - closed savanna	112	-0.059

Table 15. Spearman rank correlation coefficients (r) of wind speed with *O. jutta* abundance (individuals/hr) and estimated percent tree canopy on peak unit surveys ($N = 603$) per site per year during 2002–11, by bog type. Only sites in northern Wisconsin where we recorded *O. jutta* are included for analysis.

	<i>O. jutta</i> abundance			Percent tree canopy		
	N	r	P	N	r	P
Muskeg	367	-0.209	< 0.01	358	-0.430	< 0.01
Kettlehole	42	+0.019	> 0.10	42	-0.168	> 0.10
Coastal peatland	18	+0.453	< 0.10	18	+0.595	< 0.01
Unclassified acid peatland	193	-0.137	< 0.10	185	-0.289	< 0.01

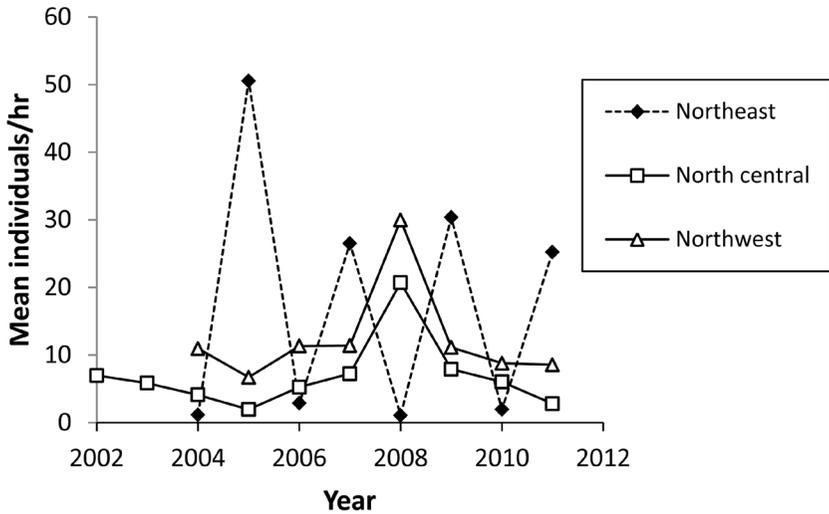


Figure 1. Regional abundance per year (mean *O. jutta* individuals per hr on unit surveys on peak survey per year in muskeg sites surveyed each year from 2002 or 2004 through 2011), by subregion in northern Wisconsin. Nearest sites between subregions: 90 km (northeast and north central) and 117 km (north central and northwest).

Table 16. Mean *O. jutta* per hour on unit surveys, and mean percent years unobserved per site, on peak survey per year for sites surveyed every year during 2004–11 and 2006–11, by odd and even years.

	<i>O. jutta</i> /hour ¹		mean % years ²	
	Odd	Even	Odd	Even
2004–2011				
Northeast (5 sites in Forest, Oneida Cos.)	32.84	1.74	10	70
North central (5 sites in Ashland, Price Cos.)	5.09	9.01	40	15
Northwest (5 sites in Douglas Co.)	9.50	15.01	10	0
2006–2011				
Coastal Bayfield peatlands (2 sites)	2.75	1.88	50	50
Inland Bayfield kettleholes (3 sites)	2.33	2.58	56	44
Central (1 site in Jackson Co.)	7.62	10.83	0	0

¹Difference in abundance between odd and even years is significant only in Northeast (Mann-Whitney *U* test $P < 0.0001$ for both 2004–2011 and 2006–2011).

²Within study period, difference among subregions in percent years not observed only significant in 2004–11 in even years

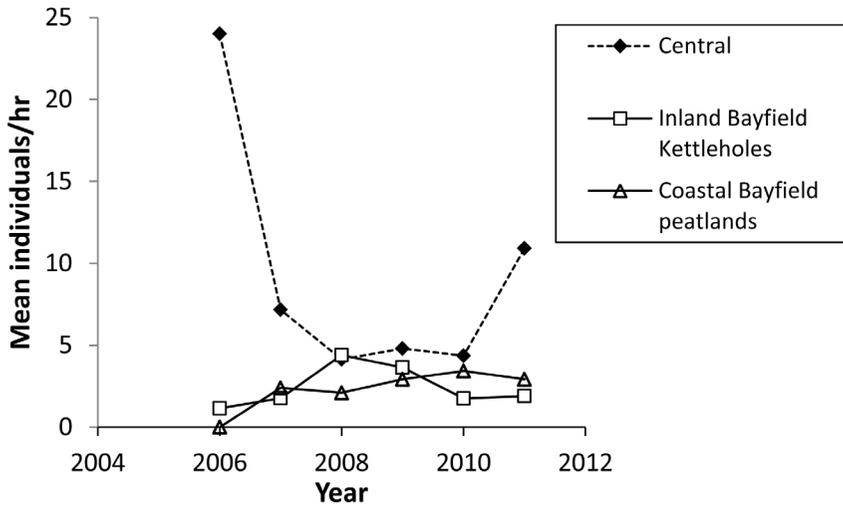


Figure 2. Regional abundance per year (mean *O. jutta* individuals per hr on unit surveys on peak survey per year on coastal Bayfield peatlands, inland Bayfield kettleholes, and one Jackson County acid peatland surveyed each year from 2006 through 2011). Nearest sites between subregions: 46 km (coastal and interior Bayfield) and 169 km (central to north central in Fig. 1).

Table 17. Mean value of each weather and time of day variable by odd and even years in northeastern Wisconsin on peak unit surveys per site per year during 2004–2011 at five long-term monitoring sites (Fig. 1). Two-tailed P values are provided from Mann-Whitney *U* tests between odd and even years.

	Odd years	Even years	<i>P</i>
Cloud cover (%)	58.0	46.3	> 0.10
Percent sunshine	40.7	58.8	< 0.10
Temperature (°C)	20.9	22.5	= 0.01
Wind speed (km)	5.7	9.7	< 0.05
Time of day	11:57	10:55	> 0.10
Crepuscularity ¹	3:00	2:22	> 0.10

¹mean time since noon standard time

Observed flight spans in our study were lengthened in 5/6 subregions (all except inland Bayfield kettleholes) when we found very early *O. jutta* in 2010, which is after the Michigan dataset closed in Nielsen (1999) and (Perkins 2007) (earliest date 20 May in both). In the three analyzable subregions of northern Wisconsin, northeast had the shortest flight span per year as measured by the mean, median, and minimum spans recorded but not the maximum (Table 3). This may result from the consistently very low abundance and 70% survey counts of zeros in half of years (Fig. 1, Table 16), even though there was no statistical relationship between flight span and number of individuals recorded per year in any subregion (Table 3).

Habitat Associations. *O. jutta* was more abundant in muskegs than kettleholes and coastal peatlands (Table 6), even when controlling for size (Table 11). But the muskegs in this study were significantly more canopied than the kettleholes and coastal peatlands (Table 11), and *O. jutta* significantly increased in each bog type as canopy increased (Table 8, 9). *O. jutta* is widely reported to associate with trees, groves, and forested areas (Ebner 1970, Ferris and Brown 1989, Nekola 1998, Nielsen 1999). The dramatic variation by even and odd years (Table 16) that resulted in a higher standard deviation in observation rates (Table 10) in northeast Wisconsin contributes to that subregion having no statistical difference in mean *O. jutta* abundance from both the subregion where *O. jutta* was significantly more abundant (northwest) and significantly less (north central) (Table 6).

Effect of patch size was mixed. In kettleholes, which were all small and had relatively little variation in size, both *O. jutta* and tree canopy increased with increasing patch size (Table 12). But in muskegs, which had a greater range in size and higher abundance of *O. jutta*, these correlations were negative (Table 12). Site sizes of both muskegs and kettleholes were more highly correlated (negatively or positively) with tree canopy than with *O. jutta* abundance, and in the same direction (negative or positive) as the correlation with *O. jutta* abundance (Table 12). Thus, canopy may be the primary explanation for *O. jutta*'s unusual pattern relative to patch size in muskegs. Our results suggest that in this sample, larger muskegs had more local variation in canopy cover, and lower overall canopy, with *O. jutta* preferentially occupying the more canopied groves and patches. That is, the large bog study sites may consist of a set of small and patchy habitats for *O. jutta*. Since we did not select sites randomly in this study, it is unknown whether this pattern applies more generally to Wisconsin peatlands.

Correlations of *O. jutta* abundance to wind were weaker than correlations of canopy to wind, but were in the same direction (usually negative). This suggests that canopy is the stronger influence on *O. jutta* abundance rather than wind. The underlying driver is unclear: *O. jutta* adults may prefer shelter from wind, or more canopied habitat may be more suitable habitat that also happens to be more sheltered from wind than opener bogs.

We found *O. jutta* in very small isolated bogs (Table 7), although not necessarily frequently. However, *O. jutta* showed virtually no tendency to venture out of bogs, since we very rarely found it in roadsides (abundance rates were 15 times as high in non-roadside sites in Table 1), and only when the road bisected a peatland occupied by the butterfly, and never farther away from a peatland. The ability of some specialists to maintain populations in small sites was well documented by Thomas (1984). In our surveys, two of Wisconsin's eight bog-specialist butterflies, bog copper *Lycaena epixanthe* (Boisduval and LeConte) and bog fritillary *Boloria eunomia* (Esper), had their highest abundance in small sites, most of which were isolated (Swengel and Swengel 2011).

The correlation between transect surveys (as done in this study) and methods estimating population size may not co-vary between different parts of a single site (Harker and Shreeve 2008). However, when these methods are

compared across a range of sites or subsites, strong concordance of results has been reported (Mattoni et al. 2001). When Thomas (1983) validated a single transect survey through core habitat of the butterfly species during main flight period to mark-release-recapture results, he concluded that an even more approximate survey method would rank the abundance of different populations adequately. Likewise, similar rankings of population abundance have occurred between weekly transect counts and line-transect extrapolations (Brown and Boyce 1998, Isaac et al. 2011). One purpose of estimating population size is to address the bias in results among different observers (Isaac et al. 2011; Bried et al. 2012). But since the observers were the same on all surveys in this study, that problem is not applicable to this study. Another purpose of methods estimating population size is to account for possible impacts of variation in vegetation among sites that might affect detectability of butterflies. Increased brush and trees could reduce detectability of butterflies by obscuring views of them. However, this factor did not significantly relate to results in Brown and Boyce (1998) or Isaac et al. (2011) and in this study, observation rates of *O. jutta* were higher in association with more canopy (Tables 8, 9).

Annual Variation. In most Wisconsin subregions, variation in abundance among years did not show a marked pattern by even and odd years (Figs. 1–2, Table 16). Instead, this variation appeared to relate only to the annual fluctuations reported for butterflies generally (Thomas 1984, Swengel 1990, Pollard and Yates 1993, Swengel and Swengel 2010, Johnson 2011). However, in addition to these fluctuations, the northeast subregion (just 90 km from the north central subregion) also exhibited dramatic variation in *O. jutta* abundance between even and odd years (Fig. 1, Table 16). While the difference in wind between even and odd years on the surveys at long-term sites in northeast Wisconsin was significant, this difference was relatively minor compared to the extreme variation in *O. jutta* abundance between even and odd years. Furthermore, the maximum wind on any of these surveys was 24 km/hr, within the allowable range in other butterfly survey programs (van Swaay et al. 2008). Thus, it is unlikely that this dramatic variation in *O. jutta* abundance between even and odd years can be attributed to weather conditions on surveys. This is consistent with reports that *O. jutta* flies mainly in odd years in Wisconsin (Kuehn 1983) and adjacent Michigan (Nielsen 1999). Nonetheless, the species was discovered in Wisconsin in 1954 (Ebner 1970), reported in the Upper Peninsula of Michigan on 20 May 2006 (Perkins 2007), and occurred in analyzable numbers in northwestern Wisconsin in 1996 (Nekola 1998, Nekola and Kraft 2002). Even-year reports of *O. jutta* occur regularly in Wisconsin, including in northeast Wisconsin (Langlade County in 1988) but much more often in north central and northwest (e.g., 1998, 2000, 2002, 2004) (Wisconsin Entomological Society season summaries published in 1989, 1999, 2001, 2003, 2005).

Oeneis jutta is reported to have a two-year life cycle (Opler and Krizek 1984, Scott 1986). In many areas of North America, *O. jutta* consistently varies in abundance between even and odd years, but regions differ as to whether *O. jutta* is found mostly or only in even years (e.g., westward in Canada) or odd years (e.g., eastward in Canada), or about the same in both (e.g., centrally in Canada) (Opler and Krizek 1984, Scott 1986, Klassen et al. 1989, Layberry et al. 1998). This pattern can vary across relatively short distances (Scott 1986, Ferris and Brown 1989). Both Scott (1986) and Klassen et al. (1989) indicate variation in the immature stage in the first winter (1st-3rd instar larva) and the second winter (4th-6th instar larva or occasionally pupa) for *O. jutta*. It is unclear whether this variation in rate of development occurs only among regions or also within region but suggests the possibility that non-biennial generations could occur. Where *O. jutta* adults are found regularly in both even and odd years, as in all of the Wisconsin range, it could be difficult to determine whether the even and odd years contain distinct cohorts or whether there is any mixing between the cohorts.

Applications to Butterfly Population Biology. *O. jutta* populations in central and northern Wisconsin present a natural experiment for understanding how localized butterfly populations may function in a fragmented landscape. Swengel and Swengel (2011) described how bog-specialist butterfly populations occurred not only in metapopulations (larger populations in larger and/or more connected habitat patches) but also with small numbers thinly spread in larger sites or with large numbers in small, isolated sites. *O. jutta* also occurs in low-density populations apparently persisting in small, isolated sites. Outside peatlands, when a localized butterfly species is occasionally but not consistently found in a site, this may be attributed to straying in from some other location, even though a known source within likely dispersal distance may not be known (many lepidopterists pers. comm., including us). This could be the case. However, butterflies in isolated populations, including strong fliers in bog/fen habitats, commonly exhibit very little tendency to disperse out of the habitat patch (Thomas 1984, Schtickzelle and Baguette 2003), and adult bog-specialist Lepidoptera are typically found in the same subhabitat within the bog where their larvae develop (Väisänen 1992). Peatland butterfly dispersal tendency decreases as isolation and fragmentation increase (Baguette et al. 2003, Schtickzelle et al. 2006), and the fossil record documents relative faunistic stability in isolated peatlands (Spitzer and Danks 2006, Whitehouse 2006, Whitehouse et al. 2008). As a result, another possibility exists. These small isolated sites may in fact support small populations of *O. jutta* that are relatively difficult to observe.

If so, a great deal of survey effort may be necessary to distinguish transient incidence in an area from a low-density resident population that is difficult to find. In the latter situation, habitat quality— as defined specifically for a butterfly as the particular resources and conditions they require (Longcore et al. 2000, Dennis and Hardy 2007, Turlure et al. 2009, Dennis 2010)— would be more important for persistence of specialist butterfly populations than landscape configuration of patch size and connectedness, although both contribute (Baguette et al. 2011, Thomas et al. 2011). As a result, a focus in conservation actions on consistent retention of specialist populations within sites, including small and isolated ones, may be more effective for long-term butterfly persistence than relying on rescue via recolonization from other populations, which may or may not be effectively dispersing out into the landscape. Under this scenario, striving to maintain stable conditions at isolated sites via unintensive or no land use is likely to aid in the longer-term maintenance of specialist butterflies (Kirby 1992, Dapkus 2004, Spitzer and Danks 2006, Whitehouse et al. 2008, Goffart et al. 2010, Swengel and Swengel 2010).

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