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SPATIAL SYNCHRONY IN WISCONSIN KARNER BLUE (LEPIDOPTERA: LYCAENIDAE) POPULATIONS

Scott R. Swengel[1] and Ann B. Swengel[1]

ABSTRACT

We analyzed geographic patterns of Karner blue (*Lycaeides melissa samuelis* Nabokov, Lepidoptera: Lycaenidae) population fluctuations in summer broods in central and northwestern Wisconsin and spring+summer broods in central Wisconsin. We removed possible effects of population trends by analyzing residuals from a regression of each site's population index vs. year. We then calculated correlation coefficients (r) of these residuals for all site-pairs separately for 1992-2005 (26 sites, N = 325 site-pairs), 1995-2005 (21 sites, N = 210), and 1998-2005 (14 sites, N = 91). We analyzed patterns in these r values relative to distance between sites using correlations vs. distance and using pairwise comparisons of different distance categories (0-3 km up to 223-264 km apart). Karner blues showed significant ($P < 0.05$) population synchrony over all distances. Spatial autocorrelation was strongest among sites <3 km apart, then gradually leveled off at greater distances. Statistical power increased when we added three years but the number of sites did not decrease greatly (1995-2005 vs. 1998-2005 analyses) and when using an annual index combining spring+summer indices instead of just summer. The spatial autocorrelation extending over the entire study region suggests that environmental factors like weather provide some synchronization of Karner blue populations. Their much higher local synchrony is consistent with the species' short dispersal distance. Their local and regional spatial autocorrelation increases the likelihood of correlated local extinctions during low fluctuation broods, especially when these coincide with unfavorable weather or adverse habitat events.

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The Karner blue (*Lycaeides melissa samuelis* Nabokov, Lepidoptera: Lycaenidae) is restricted to eastern North America. It has two complete life cycles per year (spring and summer "broods" or generations), feeds only on wild lupine (*Lupinus perennis* L., Fabaceae) as a larva, and overwinters as an egg. This butterfly has a geographically narrow, generally east-west historical range at the northern end of lupine range, from eastern Minnesota through the Great Lakes states and southern Ontario to New England. The Karner blue was federally listed as endangered in the U.S. in December 1992. It is considered extirpated in Canada. A federal recovery plan for the Karner blue was approved in 2003, which designated five recovery units in Wisconsin (Iftner et al. 1992, Bleser 1993, Dirig 1994, Packer 1994, Savignano 1994, U.S. Fish and Wildlife Service 2003).

In this paper, we analyze population monitoring results for the Karner blue in central and northwestern Wisconsin for spatial autocorrelation: the degree of synchrony in population abundance observed across geographic space, often including synchrony in population fluctuation over time (definition adapted from Koenig and Knops 1998). The persistence of Karner blue populations is likely to be linked to how much their population dynamics are correlated among habitat patches (demes) as a result of genetic exchange between nearby demes and spatially correlated environmental effects, such as weather (adapted from Sutcliffe et al. 1997).

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The more rapidly that spatial autocorrelation declines with distance, the more sedentary the butterflies in a population usually are (Sutcliffe et al. 1996). Karner blues fall at the low range of documented butterfly dispersal tendencies (Schweitzer 1994, U.S. Fish and Wildlife Service 2003). For example, Knutson et al. (1999) found a mean maximum distance between captures in Indiana of 73 m, with <10% moving >200 m. In Wisconsin, Bidwell (1995) found that 91% of recaptured males moved <400 m and 91% of females <200 m; only 3% dispersed between lupine patches (maximum of 1600 m movement). In New York, Fried (1987) found <2% of recaptured Karner blues in different lupine patches than where they started (maximum of 460 m movement).

The results of our spatial autocorrelation analysis will be useful for Karner blue conservation, by providing additional information for assessing the risk of population extirpation. The greater the distance over which populations remain significantly correlated in less vagile species, the more that environmental factors (e.g., weather) are implicated as important causes of population fluctuations (Dennis 1993, Pollard 1991). Furthermore, the greater the population fluctuations over time and/or the more similar the environment these populations inhabit, the more likely a species will exhibit spatial autocorrelation (Hanski and Woiwod 1993). Such correlation increases the likelihood that populations will have simultaneous low fluctuations that reduce viability of smaller populations (Ehrlich et al. 1980, Sutcliffe et al. 1997). If environmental factors are an important influence on Karner blue fluctuations, then their synchronizing effects on abundance would exacerbate synchronizing influences due to dispersal among nearby demes in the metapopulation, thus increasing the probability of correlated population extinctions.

METHODS

Study sites and surveys

In central Wisconsin, we started population monitoring (consecutive-brood surveying of a site) for Karner blue adults in two contiguous counties (Jackson, Wood) in summer 1990 (N = 3 sites) (Table 1; Swengel and Swengel 1996). We added additional monitoring sites in the same counties in spring 1991 (N = 2 sites), spring 1992 (N = 3), spring 1993 (N = 1), spring 1994 (N = 1), spring 1995 (N = 3), and summer 1996 (N = 1). We tried to survey all monitoring sites several times within a brood, to obtain one survey as near to "peak" numbers as possible, but weather and scheduling problems prevented this at a few sites in some broods. Our surveys at other sites aided in timing surveys at monitoring sites (Swengel and Swengel 1999).

In northwestern Wisconsin (Burnett County), we consistently surveyed Karner blues only in summer. We started with 11 sites in summer 1991 (Table 1), with one site added in 1994, one in 1995, and two in 1998. We only surveyed on one date per summer brood here during the main Karner blue flight period. Our surveys in central Wisconsin and elsewhere in northern Wisconsin also aided in date selection.

All monitoring sites were occupied by Karner blues at the start of population monitoring. The three counties these sites fall in are each in a different federal recovery unit (U.S. Fish and Wildlife Service 2003). All sites within a county are nearer to each other (<25 km apart) than to any site in another county (>30 and <52 km apart between counties in central Wisconsin; >222 km and <265 km between central and northwestern Wisconsin).

We conducted transect surveys along like routes within each site each visit (similar to Pollard 1977), as described in Swengel and Swengel (1996, 2005). All butterfly species found were counted, but survey times and locations were selected to study barrens-specific butterflies, including the Karner blue. A new survey unit was designated whenever the habitat along the route varied by

Table 1. Monitoring sites in central (Jackson and Wood Counties) and northwestern Wisconsin (Burnett County). In central Wisconsin, we surveyed consecutive spring and summer broods since the first brood surveyed; in northwestern Wisconsin, consecutive summer broods.

Subregion/County/Site	First brood	Km	Latitude	Longitude
Central Wisconsin				
Jackson County				
Dike 17	1990 summer	1.45	44.31	90.564
North Brockway East	1996 summer	0.56	44.32	90.7
South Brockway West 1	1995 spring	0.28	44.281	90.742
South Brockway West 4	1991 spring	0.40	44.283	90.744
Stanton Roadside	1991 spring	1.69	44.23	90.65
West Castle Mound 2	1992 spring	0.40	44.273	90.764
West Castle Mound 4	1992 spring	0.93	44.273	90.766
West Castle Mound roadside	1994 spring	0.40	44.275	90.765
Wildcat-Spangler NE	1990 summer	0.84	44.2782	90.678
Wildcat-Spangler SE	1993 spring	0.40	44.278	90.678
Wood County				
Highway X east-west	1991 spring	0.97	44.30	90.13
Highway X north-south	1990 summer	1.61	44.34	90.13
Highway X south	1995 spring	0.46	44.32	90.13
Sandhill west field	1995 spring	0.56	44.33	90.18
Northwestern Wisconsin				
Burnett County Forest				
Peet Firebreak	1994 spring	0.40	45.905	92.543
Peet Roadside	1995 summer	0.84	45.91	92.545
Crex Meadow Wildlife Area				
James Road	1991 summer	0.56	45.875	92.55
Klots Road	1991 summer	0.64	45.88	92.55
Main Road	1991 summer[1]	0.36	45.87	92.55
North Reed Lake East	1991 summer	0.48	45.92	92.58
North Refuge Road	1991 summer	0.80	45.90	92.60
Overlook Northeast	1991 summer[1]	0.32	45.88	92.632
Overlook Northwest	1991 summer[1]	0.32	45.88	92.634
Overlook Southeast	1991 summer[1]	0.28	45.878	92.632
Overlook Southwest	1991 summer	0.44	45.878	92.634
Phantom Prairie	1991 summer	0.48	45.83	92.67
Reed Corner	1991 summer	0.56	45.905	92.55
Fish Lake Wildlife Area				
Stolte Road unit 1	1998 spring	0.28	45.738	92.74
Stolte Road unit 2	1998 spring	0.40	45.735	92.74

[1] No sampling in summer 1996 due to inclement weather.

management and/or vegetation type. For each unit, we recorded temperature, wind speed, percent cloud cover, percent time sun was shining, route distance, and time spent surveying. Data from each unit were kept separate. Surveys occurred in a wide range of weather and times of day. Our population index is the peak survey total per site per brood, divided by route distance, to create a rate of observation (or relative abundance) per km that is comparable among sites. We recorded 13778 Karner blues in 430 km of peak surveys.

Relative abundance indices derived from transect counts (single or multiple counts per site per generation) covary strongly with estimates of absolute numbers (line-transect or mark-release-recapture), both in studies of Karner blues (Brown and Boyce 1998, King 2000) and other butterflies (Pollard 1977, Thomas 1984, Mattoni et al. 2001). Relative abundance indices have the advantage of allowing more sites to be sampled in the same amount of time compared to methods for estimating absolute numbers (King 2000). Surveying more sites, with less effort allocated per site, generates more statistical power for trend detection than spending more effort in fewer sites (Cox 1990).

Statistical analyses

Because our sites varied as to when population monitoring started, we decided to compare results from more sites but fewer years of data vs. fewer sites with more years of data. Furthermore, because our sites also varied as to whether we conducted spring and summer surveys, or only summer surveys, we also compared results for the same sites using only summer data vs. using spring and summer data. For the latter, the population index was the sum of the spring and summer indices for a year (e.g., peak Karner blues per km in spring 2005 + peak Karner blues per km in summer 2005 = 2005 spring+summer index for a site). In British butterfly monitoring, a population index combining the spring and summer abundance is also used for bivoltine species (Pollard and Yates 1993). For summer-only analysis, we had 29 sites in central and northwestern Wisconsin surveyed each year during 1998-2005; for 1995-2005, 23 sites; and for 1992-2005, 15 sites (also divided into 1992-98 and 1998-2005 spans to compare shorter vs. longer time spans for the same sites). For spring+summer analysis, we had 14 sites surveyed in central Wisconsin in each brood during 1998-2005; for 1995-2005, 13 sites; and for 1992-2005, 8 sites (again, also divided into 1992-98 and 1998-2005 spans). Within type of analysis (summer only or spring+summer), all 1992-2005 sites were in the pool for 1995-2005, which in turn were all in the pool for 1998-2005. All these pools surpass the standard of using at least seven years of overlapping data (Hanski and Woiwod 1993). Since all sites in each analysis had surveys for all broods in that analysis, we did not need to perform corrective measures for missing survey values.

Spatial autocorrelation analysis is analogous to isolation-by-distance (IBD) genetic analysis (Slatkin 1993, Peterson and Denno 1998, Bohonak 2002, Walter and Epperson 2005) but spatial autocorrelation analysis can have two preparatory steps before performing the correlations (Sutcliffe et al. 1996, Koenig and Knops 1998, Koenig 2006). First, sites with only very low counts are eliminated. We dropped sites with zero as >25% of the population indices. For summer-only analysis, that resulted in 26 sites for 1998-2005, 21 for 1995-2005, and 14 for 1992-2005. For spring+summer analysis, that left 13 sites for 1998-2005, 12 sites for 1995-2005, and all 8 sites for 1992-2005. Second, the population indices are detrended. We did a base-10 logarithmic transformation of these indices to make them suitable for parametric analysis. Then for each set of years, we did a separate linear regression of these transformed indices vs. year for each site. These indices were plotted by year and a straight line fitted through them. The amount each index deviated above or below this trend line is the residual (each year's actual population index minus the "expected" index for that site and year based on the site's regression line fitted to those indices vs. year). The residuals constitute population indices that have the variability from any possible long-term population trend at the site removed from them.

Spatial autocorrelation analysis can also be performed on "trended" data. Buonaccorsi et al. (2001), Liebhold et al. (2004), and Royama (2005) reviewed trended and detrended analytical techniques. They discuss the advantages and disadvantages of each, but indicate all are acceptable approaches that address somewhat different issues. We already analyzed spatial synchrony with trended data in Swengel and Swengel (2005), although not in site-pair correlations. By using the standard detrended method here, our analysis is more comparable to Sutcliffe et al. (1996), the study most similar to ours in study species and scale, and affords the opportunity to compare detrended results here to trended results in Swengel and Swengel (2005).

Then, for every combination of site-pairs in each sample (i.e., each combination of year-span × type of index × site selection), we used the Pearson product-moment correlation to correlate the residuals from each site in the pair. The resulting correlation coefficients (*r*) become the dependent variable analyzed for spatial autocorrelation. We calculated the distance separating the two sites in each site-pair by measuring from a map for distances <52 km and using the great circle calculator (Byers 1997) for distances >222 km.

We used two different tests to determine whether these coefficients exhibited significant positive spatial autocorrelation. First, we used a binomial probability test to determine whether there was a non-random bias toward higher numbers of positive than negative coefficients in the site-pair correlations. Random distribution would be 50% positive, 50% negative. We then used the Chi-square goodness of fit test to determine whether there was a non-random bias toward significantly positive ($P < 0.05$) coefficients in the site-pair correlations vs. non-significance and/or negative significance. Random distribution would be 5% significantly positive. Observed values were the number of positive significant coefficients and number of remaining coefficients in the sample; expected values were 5% and 95% of the total number of coefficients (e.g., 325 summer-only site-pair coefficients for 1998-2005: 5% = 16.25 and 95% = 308.75). The 5% random significance expected due to Type I statistical error actually applies to both positive and negative coefficients (2.5% for each), but since our interest was whether positive coefficients were significant, we used this stricter test.

Next, we conducted two tests for variation in spatial autocorrelation vs. distance. We tested for linear change with increasing distance by using the Pearson product moment correlation to correlate the coefficients vs. distance between the sites in the site-pairs, as in IBD analysis (Slatkin 1993). We also used the Mann-Whitney U test to analyze for differences in the coefficients by distance categories: 0.25-2.99 km vs. 3.0-264, as well as 0.25-2.99, 3.0-25, 30-51, and 223-264 (no sites were 25-30 km or 51-223 km apart). For the spring+summer 1992-2005 sample, only 3 site-pairs were 0.25-2.99 km apart but no site-pairs were 3.0-3.99 km apart, and only one was 4.0-4.99 km apart. Since this did not increase sample size much, we decided to keep this smallest distance category at 0.25-2.99 km. Sutcliffe et al. (1996) found a distinct decline in butterfly spatial autocorrelation beyond 2-4 km, so our shortest category fits in that range. In addition, 3 km is about twice the Karner blue's generally observed maximum dispersal distance (Welch 1993, King 1998; see also Introduction).

We then compared our results to Sutcliffe et al.'s (1996) analysis of spatial autocorrelation within sites (0.1-5 km) and among sites (>5 up to 200 km) for 17 British butterfly species at 22 sites. They plotted the site-pair coefficients (y axis) by distance (x axis) within sites to calculate the regression line, the straight line fitted through the plotted values. This line is described by the estimated constant term (where the line intercepts the y axis) and the slope of the line toward the x axis (the regression coefficient). Since spatial autocorrelation is expected to decrease with distance, this line is expected to have a negative (declining) slope with increasing distance. They determined the

distance value at which this regression line reached the value for the overall mean of the site-pair correlation coefficients among sites for all species (plotted on the y axis) i.e., the distance at which local spatial autocorrelation decreases to the background level of spatial autocorrelation regionally. For sedentary species, the mean y-intercept was highest and mean slope decreased the fastest, reaching the regional mean at about 1.75 km. Mobile species had the lowest y-intercept and shallowest decrease in slope, reaching the regional mean at about 4 km. The results for intermediate species fell between the two but nearer to sedentary species.

We calculated the y-intercept and slope for our site-pair correlation coefficients for 0.25-2.99 km, 0.25-5.00 km, and 0.25-264 km for each sample (i.e., each combination of year-span × type of index × site selection). For comparisons to Sutcliffe et al. (1996), we used summer-only indices, since they used that type of index for bivoltine species; we averaged our values for the 1998-2005, 1995-2005, and 1992-2005 spans. We calculated y-intercepts and slopes for different distance categories. For very short-distance plots (up to 2-3 km), the y-intercept is expected to be relatively high and the slope relatively shallow in its decline, indicating relatively high spatial autocorrelation for the entire distance span. Increasing the distance a bit more (to 5 km), the y-intercept should still be relatively high but the slope relatively sharp in descent, indicating that the plot includes both the high spatial autocorrelation at very near distances but also markedly lower spatial autocorrelation beyond that. When the plot includes a large distance span, higher spatial autocorrelation at the nearest several km but lower spatial autocorrelation for most of the distances plotted would result in both a lower y-intercept and a shallower slope.

Burning was a frequent management practice, especially in Burnett County. Burning reduces Karner blue numbers in the short-term (Bleser 1993, Swengel 1995), and so could counteract synchrony in spatial autocorrelation. With the Mann-Whitney U test, we tested for differences in coefficients by whether any site in the site-pair had been burned during the year-span analyzed.

Analysis was done with ABstat 7.20 software (1994, Anderson-Bell Corp., Parker, Colorado), with statistical significance set at $P < 0.05$. Since significant results occurred much more frequently than would be expected due to Type I statistical errors, we did not lower the P value further, as many more Type II errors would then be created than Type I errors eliminated. One-tailed tests are often used in spatial autocorrelation analyses because all significant results are expected to be in the direction of greater autocorrelation at shorter distances (Koenig and Knops 1998). But we used two-tailed tests, which doubled the statistical stringency.

RESULTS

The site-pair correlation coefficients had a strong non-random positive bias (Table 2). All 15 sets of correlation coefficients, representing each combination of year-span x type of index x site selection, had non-randomly high proportions of positive values ($P < 0.005$). When broken into distance categories, six of the 50 subsets of coefficients had a sample size too small to support statistical testing. Of the remaining 44 subsets, 40 (91%) were significantly biased toward positive coefficients, four (9%) at $P < 0.05$ and 36 (82%) at $P < 0.01$.

The site-pair coefficients also had a strong bias to be positively significant at $P < 0.05$ (Table 3). Of the 15 sets of coefficients, 13 (87%) were significantly biased toward positive significance, one (7%) at $P < 0.05$ and 12 (80%) at $P < 0.01$. When broken into distance categories, 29 (58%) of the 50 subsets of coefficients were significantly biased toward positive significance, three (6%) at $P < 0.05$ and 26 (52%) at $P < 0.01$.

Table 2. Binomial distribution test for whether site-pair correlation coefficients are significantly skewed toward being positive rather than negative, for the entire sample and by four categories of distance (km) between sites.

	Summer-only index			Spring+summer index			Summer-only index same sites as spring+summer		
	N[1]	% positive	P	N[1]	% positive	P	N[1]	% positive	P
1998-2005	325	72.0	0.0000	78	92.3	0.0000	78	82.1	0.0000
0.25-2.99	31	80.6	0.0003	14	100.0	0.0000	14	85.7	0.0056
3-25	89	69.7	0.0000	28	96.4	0.0000	28	82.1	0.0004
30-51	36	80.6	0.0001	36	86.1	0.0000	36	80.6	0.0001
223-264	169	69.8	0.0000	-			-		
1995-2005	210	86.2	0.0000	66	100.0	0.0000	66	92.4	0.0000
0.25-2.99	21	100.0	0.0000	12	100.0	0.0002	12	95.5	0.0000
3-25	49	85.7	0.0000	22	100.0	0.0000	22	95.5	0.0000
30-51	36	88.9	0.0000	32	100.0	0.0000	32	87.5	0.0000
223-264	104	82.7	0.0000	-			-		
1992-2005	91	82.4	0.0000	28	100.0	0.0000	28	92.9	0.0000
0.25-2.99	6	100.0	0.0156	3	100.0	0.1250[2]	3	100.0	0.1250[2]
3-25	25	84.0	0.0004	13	100.0	0.0001	13	92.3	0.0016
30-51	12	91.7	0.0029	12	100.0	0.0002	12	91.7	0.0029
223-264	48	77.1	0.0000	-			-		
1992-1998	91	82.4	0.0000	28	100.0	0.0000	28	96.4	0.0001
0.25-2.99	6	100.0	0.0156	3	100.0	0.1250[2]	3	100.0	0.1250[2]
3-25	25	84.0	0.0004	13	100.0	0.0001	13	92.3	0.0016
30-51	12	100.0	0.0002	12	100.0	0.0002	12	100.0	0.0002
223-264	48	75.0	0.0002	-			-		
1998-2005 same sites as									
1992-1998	91	64.8	0.0015	28	92.9	0.0000	28	75.0	0.0044
0.25-2.99	6	66.7	0.2344	3	100.0	0.1250[2]	3	66.7	0.3750[2]
3-25	25	56.0	0.1328	13	100.0	0.0001	13	76.9	0.0349
30-51	12	75.0	0.0537	12	83.3	0.0161	12	75.0	0.0537
223-264	48	66.7	0.0080	-			-		

[1] Number of site-pair correlation coefficients.
[2] N too small to be able to achieve significance.

Table 3. Chi-square goodness of fit test for whether individual site-pair correlation coefficients are significantly skewed toward being significantly positive ($P < 0.05$), for the entire sample and by four categories of distance (km) between sites.

	Summer-only index			Spring+summer index			Summer-only index same sites as spring+summer		
	N[1]	%	P	N[1]	%	P	N[1]	%	P
1998-2005	325	16.3	0.0000	78	34.6	0.0000	78	19.2	0.0000
0.25-2.99	31	29.0	0.0000	14	35.7	0.0000	14	35.7	0.0000
3-25	89	18.0	0.0000	28	46.4	0.0000	28	21.4	0.0004
30-51	36	12.5	0.1936	36	25.0	0.0000	36	11.1	0.1936
223-264	169	14.2	0.0000	-			-		
1995-2005	210	22.9	0.0000	66	59.1	0.0000	66	27.3	0.0000
0.25-2.99	21	61.9	0.0000	12	75.0	0.0000	12	58.3	0.0000
3-25	49	22.4	0.0000	22	59.1	0.0000	22	22.7	0.0009
30-51	36	25.0	0.0000	32	53.1	0.0000	32	18.8	0.0016
223-264	104	14.4	0.0000	-			-		
1992-2005	91	14.3	0.0001	28	64.3	0.0000	28	21.4	0.0004
0.25-2.99	6	50.0	0.0000	3	100.0	0.1250	3	66.7	0.0003
3-25	25	16.0	0.0389	13	53.8	0.0000	13	15.4	0.2796
30-51	12	16.7	0.2332	12	75.0	0.0000	12	16.7	0.2332
223-264	48	8.3	0.4663	-			-		
1992-1998	91	11.0	0.0173	28	60.7	0.0000	28	17.9	0.0072
0.25-2.99	6	0.0	0.7079	3	33.3	0.3538	3	0.0	0.3538
3-25	25	20.0	0.0029	13	53.8	0.0000	13	23.1	0.0186
30-51	12	16.7	0.2332	12	75.0	0.0000	12	16.7	0.2332
223-264	48	6.3	0.9472	-			-		
1998-2005 same sites as									
1992-1998	91	9.9	0.0574	28	35.7	0.0000	28	7.1	0.9309
0.25-2.99	6	16.7	0.7079	3	33.3	0.3538	3	0.0	0.3538
3-25	25	12.0	0.2513	13	46.1	0.0000	13	15.4	0.2794
30-51	12	0.0	0.8946	12	25.0	0.0118	12	0	0.8946
223-264	48	10.4	0.1643	-			-		

[1] Number of site-pair correlation coefficients.

In tests for variation in site-pair correlation coefficients by distance between sites, significant results occurred less frequently but still more often than due to random Type I error (5%). In the linear test for variation in spatial correlation by distance (Table 4), significant results (4 of 15 tests, 27% significant) were always negative as expected. In categorical testing of the shortest distance group (0.25-2.99 km) vs. all remaining coefficients (3-264 km), the shortest distance group averaged higher coefficients than the further distance category in all samples large enough to support statistical testing. This difference was significant in 4 of 9 testable samples (Table 5). In tests of four distance categories, six (40%) of the 15 samples showed significant differences (Table 6). Where the nearest category was statistically testable, it averaged the highest coefficients and the furthest category the lowest. The two intermediate distance categories were not entirely consistent with this pattern (i.e., the average coefficients don't show a consistent decline from nearer to further). But all significant differences were as expected: the nearer distance group was always significantly higher than the further distance group.

We tested for other sources of variation in the coefficients. Within-county site-pair correlation coefficients (i.e., Burnett-Burnett vs. Jackson-Jackson vs. Wood-Wood) did not significantly differ by county (Mann-Whitney U test, two-tailed $P > 0.10$ for all testable samples). The coefficients were significantly higher, and P values of these coefficients lower, for spring+summer indices than for summer-only indices in all comparisons, with site-pairs held constant in each comparison (Table 7). The coefficients tended to be lower when any site in the pair had been burned during the year-span than when neither site had been burned (Table 8). For summer-only coefficients, 3 of 4 time spans showed a significant difference. For the spring+summer indices, which did not include northwestern Wisconsin, sample size was much lower and no significant differences were detected.

We also compared 1992-2005 results to those for the same site-pairs for 1992-98 and 1998-2005. In Table 5, 1992-2005 summer-only indices achieved statistically significant differences while 1992-98 and 1998-2005 did not. The other comparisons in this table were not statistically testable for all these year-spans. In Table 6, the 1992-2005 and 1992-98 summer-only tests (first column) had comparable statistical results but the 1998-2005 tests had non-significant results. The sample was inadequate to test the nearest distance category for the spring+summer index, but the other distance categories showed no significant results for any of these year-spans. For the correlations of site-pair coefficients vs. distance (Table 4), the 1998-2005 year-span usually had weaker correlations than 1992-2005 but 1992-98 did not. In all these tables, the 1995-2005 sample, which had an intermediate number of years and number of sites, appeared to achieve the most statistical significance.

Table 9 presents the y-intercepts and slopes for the regression lines fitted to the site-pair correlation coefficients for each combination of year-span × type of index × site selection. In comparison to slopes for 0.25-264 km plots, slopes for 0.25-5.0 km plots were significantly steeper (Wilcoxon signed rank test two-tailed $P = 0.0026$) and for 0.25-2.99 km plots were nearly significantly so ($P = 0.0535$). The 0.25-2.99 km slopes did not differ significantly from the 0.25-5.0 km slopes. As expected, the y-intercepts tended to be lower and the slopes shallower for the 0.25-264 km plots than for the shorter-distance plots. Furthermore, as expected, the slopes tended to be steeper for the 0.25-5.0 km plots than for the 0.25-2.99 km plots.

For comparison to Sutcliffe et al. (1996: Fig. 5), we calculated the unweighted grand mean y-intercept for the summer-only regressions of r values vs. distance for the 1998-2005, 1995-2005, and 1992-2005 samples. For distances of 0-5 km (similar to Sutcliffe's short-range analysis for slope-intercept) the mean y-intercept for r was +0.56 and mean slope was -0.0849/km. In contrast, the same regression over 0-2.99 km has a y-intercept of 0.50 and a

Table 4. Pearson's product moment correlation of site-pair correlation coefficients (*r*) vs. distance between sites.

	N site-pairs	*r*	*P*
Central & Northwestern (summer only)			
All sites			
1998-2005	325	-0.0505	0.3643
1995-2005	210	-0.2195	0.0014
1992-2005	91	-0.1895	0.0721
1992-1998	91	-0.2765	0.0080
1998-2005 same sites as 1992-1998	91	+0.0601	0.5715
Central Wisconsin (summer only)			
1998-2005	78	-0.0572	0.6192
1995-2005	66	-0.1516	0.2243
1992-2005	28	-0.0505	0.7985
1992-1998	28	+0.0174	0.9301
1998-2005 same sites as 1992-1998	28	+0.0175	0.9295
Central Wisconsin (spring & summer)			
1998-2005	78	-0.2545	0.0246
1995-2005	66	-0.2899	0.0182
1992-2005	28	-0.2191	0.2626
1992-1998	28	+0.2978	0.1238
1998-2005 same sites as 1992-1998	28	-0.2608	0.1802

Table 5. Mann-Whitney U test for differences in site-pair correlation coefficients (*r*) by two categories of distance between sites.

	Summer-only index			Spring+summer index			Summer-only index same sites as spring+summer		
	N	mean *r*	*P*[1]	N	mean *r*	*P*[1]	N	mean *r*	*P*[1]
1998-2005									
0.25-2.99 km	31	+0.3717	A	14	+0.5322	A	14	+0.4256	A
3-264 km	294	+0.2386	A	64	+0.4996	A	64	+0.3060	A
1995-2005									
0.25-2.99 km	21	+0.5766	A	12	+0.7210	A	12	+0.5649	A
3-264 km	189	+0.3121	B	54	+0.5788	B	54	+0.3673	B
1992-2005									
0.25-2.99 km	6	+0.4449	A	3	+0.6718	A[2]	3	+0.4848	A[2]
3-264 km	85	+0.2246	B	25	+0.5541	A	25	+0.3142	A
1992-1998									
0.25-2.99	6	+0.4866	A	3	+0.7563	A[2]	3	+0.6383	A[2]
3-264 km	85	+0.3002	A	25	+0.7609	A	25	+0.4929	A
1998-2005 same sites as **1992-1998**									
0.25-2.99 km	6	+0.1818	A	3	+0.3801	A[2]	3	+0.0953	A[2]
3-264 km	85	+0.1390	A	25	+0.7609	A	25	+0.1816	A

[1] Within column and year-span, means not sharing the same letter(s) are significantly different (two-tailed *P* < 0.05).
[2] N too small to be able to achieve significance.

Table 6. Mann-Whitney U test for differences in site-pair correlation coefficients (*r*) by four categories of distance between sites.

	Summer-only index			Spring+summer index			Summer-only index same sites as spring+summer		
	N	mean *r*	*P*[1]	N	mean *r*	*P*[1]	N	mean *r*	*P*[1]
1998-2005									
0.25-2.99 km	31	+0.3717	A	14	+0.5322	AB	14	+0.4256	A
3-25 km	89	+0.2335	A	28	+0.6137	A	28	+0.3085	A
30-51 km	36	+0.3040	A	36	+0.4108	B	36	+0.3040	A
223-264 km	169	+0.2274	A	-	-				
1995-2005									
0.25-2.99 km	21	+0.5766	A	12	+0.7210	A	12	+0.5649	A
3-25 km	49	+0.3320	BC	22	+0.6306	AB	22	+0.3640	B
30-51 km	36	+0.4052	B	32	+0.5431	B	32	+0.3696	B
223-264 km	104	+0.2705	C	-	-				
1992-2005									
0.25-2.99 km	6	+0.4449	A	3	+0.6718	A[2]	3	+0.4848	A[2]
3-25 km	25	+0.2366	AB	13	+0.5656	A	13	+0.3004	A
30-51 km	12	+0.3292	AB	12	+0.5417	A	12	+0.3292	A
223-264 km	48	+0.1921	B	-	-				
1992-1998									
0.25-2.99 km	6	+0.4867	AB	3	+0.7563	A[2]	3	+0.6383	A[2]
3-25 km	25	+0.3613	AB	13	+0.6988	A	13	+0.4672	A
30-51 km	12	+0.5207	A	12	+0.8280	A	12	+0.5207	A
223-264 km	48	+0.2132	B	-	-				
1998-2005 same sites as									
1992-1998									
0.25-2.99 km	6	+0.1818	A	3	+0.3801	A[2]	3	+0.0953	A[2]
3-25 km	25	+0.0821	A	13	+0.5987	A	13	+0.1969	A
30-51 km	12	+0.1651	A	12	+0.3833	A	12	+0.1651	A
223-264 km	48	+0.1622	A	-	-				

[1] Within column and year-span, means not sharing the same letter(s) are significantly different (two-tailed *P* < 0.05).
[2] N too small to be able to achieve significance.

Table 7.   Mann-Whitney U test for differences in site-pair correlation coefficients (r) and P values between summer-only and spring+summer indices.

	N	Mean, summer-only	Mean, spring+summer	P [1]
1998-2005				
r	78	+0.327466	+0.505439	0.0017
P	78	0.358341	0.248205	0.0057
1995-2005				
r	66	+0.403256	+0.604608	0.0000
P	66	0.304041	0.115450	0.0000
1992-2005				
r	28	+0.332512	+0.566726	0.0000
P	28	0.314275	0.072460	0.0000
1992-1998				
r	28	+0.760365	+0.508447	0.0000
P	28	0.084543	0.27909	0.0000
1998-2005 same sample of sites as **1992-1998** sample				
r	28	+0.482996	+0.172384	0.0000
P	28	0.274239	0.460575	0.0062

[1] P values presented are one-tailed because it was not possible for us to calculate the two-tailed value for 0.0000. All tests are significant at two-tailed $P < 0.05$.

Table 8.   Mann-Whitney U test for differences in site-pair correlation coefficients (r) by whether any site in the pair had or had not been burned during the study period.

	Summer-only index			Spring+summer index		
	N	mean r	P [1]	N	mean r	P [1]
1998-2005						
burned	205	+0.195742	A	12	+0.507018	A
not burned	120	+0.346216	B	66	+0.505153	A
1995-2005						
burned	119	+0.306724	A	11	+0.547326	A
not burned	91	+0.380179	A	55	+0.616064	A
1992-2005						
burned	55	+0.186907	A	0		
not burned	36	+0.318804	B	28		
1992-1998						
burned	55	+0.224546	A	0		
not burned	36	+0.446834	B	28		

[1] Within column and year-span, means not sharing the same letter are significantly different (two-tailed $P < 0.05$).

Table 9. Sample of site-pairs (N), y-intercept, and slope for linear regression line (least squares) of site-pair coefficients to distance, for three ranges of distance between sites. Mean site-pair correlation coefficients (r) for >5-264 km distance indicate background (regional) autocorrelation.

| | 0.25-2.99 km | | | 0.25-5.00 km | | | 0.25-264 km | | | >5-264 km |
	N	intercept	slope	N	intercept	slope	N	intercept	slope	mean r
Summer only										
1998-2005	31	+0.39	-0.0097	55	+0.45	-0.0813	325	+0.28	-0.0002	+0.255
1995-2005	21	+0.57	+0.0015	37	+0.64	-0.0683	210	+0.42	-0.0006	+0.313
1992-2005	6	+0.53	-0.0458	11	+0.57	-0.1051	91	+0.30	-0.0004	+0.232
1992-1998	6	+0.77	-0.1635	11	+0.67	-0.0838	91	+0.43	-0.0009	+0.295
1998-2005[1]	6	+0.17	+0.0087	11	+0.28	-0.1089	91	+0.11	+0.0002	+0.164
Mean		+0.49	-0.0418		+0.52	-0.0895		+0.31	-0.0004	+0.252
Spring+summer										
1998-2005	14	+0.49	+0.0251	21	+0.52	+0.0006	78	+0.61	-0.0042	+0.498
1995-2005	12	+0.78	-0.0420	16	+0.76	-0.0273	66	+0.68	-0.0029	+0.593
1992-2005	3	+0.78	-0.0651	4	+0.78	-0.0655	28	+0.61	-0.0018	+0.556
1992-1998	3	+1.01	-0.1587	4	+0.82	-0.0145	28	+0.69	+0.0027	+0.755
1998-2005[1]	3	-0.01	+0.2484	4	+0.25	+0.0406	28	+0.59	-0.0044	+0.507
Mean		+0.61	+0.0015		+0.63	-0.0132		+0.64	-0.0021	+0.582
Summer only[2]										
1998-2005	14	+0.47	-0.0272	21	+0.46	-0.0299	78	+0.35	-0.0011	+0.305
1995-2005	12	+0.57	-0.0022	16	+0.59	-0.0175	66	+0.45	-0.0019	+0.358
1992-2005	3	+0.58	-0.0582	4	+0.61	-0.0811	28	+0.35	-0.0006	+0.317
1992-1998	3	+0.74	-0.0664	4	+0.73	-0.0553	28	+0.50	+0.0003	+0.492
1998-2005[1]	3	+0.24	-0.0891	4	+0.18	-0.0470	28	+0.16	+0.0003	+0.188
Mean		+0.65	-0.0486		+0.51	-0.0462		+0.36	-0.0006	+0.332
Mean of all		+0.54	-0.0296		+0.55	-0.0496		+0.44	-0.0010	+0.389

[1] Same sample of site-pairs as for 1992-1998 in previous line.
[2] Same sample of site-pairs as for spring+summer indices.

slope of only -0.018/km, confirming that Karner blue autocorrelation didn't change much for the first 3 km but dropped sharply beyond that. Our y-intercept (for 0-5 km analysis) falls nearest to their y-intercept for intermediate species (i.e., not sedentary or mobile), and our slope falls nearest to theirs for mobile species. Our slope intersects our regional (background) mean coefficient (+0.267) for >5.0-264 km site-pairs at about 3.25 km, just beyond our shortest distance group of 0-2.99 km. Their mean regional coefficient (for all species) was about +0.29, and sedentary species reached that at about 1.75 km, intermediate at about 2.0 km, and mobile at about 4.0 km.

DISCUSSION

About 80% of summer-only, and >95% of spring+summer, correlation coefficients between site-pairs were positive (Table 2). About 15% of summer-only and 19% of spring+summer coefficients were significantly positive ($P < 0.05$), far more than expected (Table 3). This indicates a high rate of background (regional) spatial autocorrelation in our Karner blue sites across a span of 264 km. The high annual variability in Karner blue populations (Swengel and Swengel 1996, Knutson et al. 1999, Lane and Andow 2003) probably contributed to the relative ease of detecting significant autocorrelation.

Swengel and Swengel (2005) also analyzed for synchrony of fluctuations. But in that analysis, the population indices for all sites in a county were averaged into a "brood index", and those brood indices (not detrended) were nonparametrically correlated among counties, rather than among pairs of sites. In that paper, the use of trended data had the effect of increasing the positive correlation of near sites (<52 km apart, between counties in central Wisconsin) and decreasing the correlation of further sites (>222 km apart, between central and northwestern Wisconsin). When the different long-term population trends occurring in northwestern and central Wisconsin (Swengel and Swengel 2005) were removed in this analysis, an underlying synchrony of fluctuations was revealed that the trends masked.

Population fluctuations showed relatively high synchrony over small distances (<3 km) (Tables 5, 6, 9), indicating strong local synchrony above regional background levels. Beyond 3 km, autocorrelation gradually leveled off at greater distances. This agrees with Sutcliffe et al.'s (1996) finding that low-mobility butterflies have high spatial autocorrelation at very short distances that declines very quickly with increasing distance to regional background levels. Strong local population synchrony is not surprising given that Karner blue populations are significantly denser ($P < 0.01$) in places with other nearby populations, called lupine "cores" in Swengel and Swengel (1996) -- i.e., places in a landscape context of numerous other lupine patches within 2 km. Numerous other studies have also demonstrated a general pattern that butterfly populations are larger when other populations are nearer rather than farther, or that habitat quality and intersite distance interact to determine butterfly patch occupancy (Harrison et al. 1988, Hanski et al. 1994, Dennis and Eales 1999, Thomas et al. 2001, WallisDeVries 2004). Although most marking studies have found that only a few Karner blues per brood move to new patches (see literature cited in Introduction and Methods), this appears adequate to raise local population synchrony above regional levels. But beyond 3 km, their relatively low mobility does not facilitate population synchrony much higher than the regional background level.

By contrast, Schultz and Hammond (2003) did not find a significant change in spatial synchrony by distance in a single-brooded blue (ca. 65% of site-pair correlations were positive and 9% of r values significant) in an 8-10 year study at 12 sites. Only about 6 of their 66 site-pairs were <5 km apart, which probably hindered detection of short- vs. long-distance differences. The Karner blue appears to fit the sedentary group in Sutcliffe et al. (1996) but its spatial autocorrelation statistics are more similar to theirs for intermediate-mobility

British species (in slope) and mobile species (distance where regional mean is reached). Several factors may contribute to this disparity. Just as more thorough surveying within a site decreases the variance in a site's annual population indices (Sutcliffe et al 1996: Fig. 3), so do more survey visits within a brood (Brown and Boyce 1998). Thus, British population indices are more robust, as they sum weekly counts throughout the brood vs. our single peak survey. This should make their site-pair coefficients higher and slopes of r values vs. distance steeper. The baseline autocorrelation that extends to at least 264 km in Karner blues indicates that similar environmental conditions create some of the synchrony (Pollard 1991). Even though our study spanned more distance than Sutcliffe et al.'s (1996) (264 vs. 200 km), the Karner blue's range in Wisconsin falls in a very uniform climatic range, which follows the tension zone defined by Curtis (1959) for plants. This tension zone correlates with similar growing season weather. Wisconsin also has a continental climate, which would be expected to show more extreme variation than England's maritime climate. More dramatic climatic variation could result in more dramatic butterfly fluctuations (e.g., Ehrlich et al. 1980), which, combined with relatively uniform climate in the Karner blue's range, could result in stronger spatial autocorrelation over longer distances than in Sutcliffe et al.'s (1996) sedentary species.

Ranta et al.'s (1995) review shows how synchrony of modeled populations due to regional environmental effects, although positive over a wide area, may not change much with increasing distance; instead, local population dynamics usually account for most of the increase in synchronization at close distances. Forest moths exhibit strong within-species spatial autocorrelation that declines with distance (Raimondo et al. 2004a). Moths in both North America and Europe also exhibit significant population synchrony among different species (Raimondo et al. 2004a,b). Both intra- and interspecific population synchrony appear largely mediated by weather but interspecific synchrony was most likely among species in which caterpillars fed in similar ways or at the same time of year (Raimondo et al. 2004a,b). Koenig (2006) found similarities in spatial synchrony of monarchs (*Danaus plexippus* (L.), Lepidoptera: Danaidae) and temperature.

The site-pair coefficients tended to be lower when any site in the pair had been burned. This is likely due to fire-caused mortality (Bleser 1993, Swengel 1995), which is independent of population fluctuations. The Karner blue's high regional spatial autocorrelation has implications for recovery from fire. A population lowered by fire might be retarded in recovery in low fluctuation years (e.g., Labus et al. 2002 after wildfire). Recovery from fire would be variable and unpredictable as a result of fluctuations, which can't be known at the time of burning but which affect ability and time required to recover.

The decline in gene flow with increasing distance in IBD studies (Slatkin 1993) is analogous to the decline in spatial autocorrelation of populations with distance, but without the background environmental synchrony of autocorrelation. IBD compares cumulative changes in genomes over many generations, however. Peterson and Denno (1998) found significant declines in gene flow with distance in 6/12 butterflies studied over maximum inter-site distances of 400-4000 km. The behavior of a species' IBD statistics over short distances should bear some relationship to the species' dispersal behavior. In a review of IBD traits of insects analyzing gene flow over spatial scales of 200-4135 km (which damps out effects that are strictly local), Peterson and Denno (1998) found that, compared to moderately mobile and highly mobile species, sedentary species had intermediate slopes (lower than moderately mobile, higher than highly mobile) and lower intercepts of gene flow vs. distance. They argue that gene flow in sedentary species is not sufficient to prevent populations tens of km apart from becoming nearly as genetically isolated as much more distant ones.

Karner blue genetic data and our results are consistent with a hypothesis that a large proportion of its spatial autocorrelation results from environmental factors instead of gene flow. In a study of North American *Lycaeides*, including

Karner blues from Minnesota, Wisconsin, Indiana, Michigan, New York, and New Hampshire (>1700 km span), Nice et al. (2000) found significant IBD patterns in geographic vs. genetic distance in microsatellite DNA. Karner blue gene flow appears to be low relative to other Lepidoptera (Packer et al. 1998), which is consistent with its relatively low dispersal. Further demonstrating that local gene flow is much greater than regional, 75.9% of isozyme variability and 66.4% of mitochondrial DNA (mtDNA) variability in *Lycaeides melissa* (W.H. Edwards) and *L. idas* (L.), northern blue, was explained by variation among populations of the same species, rather than among individuals within a population or among species (Nice and Shapiro 1999, Nice et al. 2005). When these taxa were grouped by mtDNA population clusters (independent of their species/subspecies), 90.4% of mtDNA variation was explained by differences among regions rather than within or among populations within a region (Nice et al. 2005). In Karner blues, spatial autocorrelation slopes over the entire span (0.25-264 km) of our study were very low, being high only at short distances (0.25-5 km). This pattern is consistent with those in measures estimating their gene flow. However, relatively greater synchrony of Karner blue abundance occurs over longer distances than does gene flow. This is probably because environmental factors synchronize populations on a much larger scale that is affected by gene flow.

Our analyses indicated some strategies for improving statistical power. Spring+summer coefficients were much higher than summer only, indicating that the two broods combined produce a much more robust annual index than just summer counts. This is consistent with the discussion (above) that an index calculated from multiple counts at the site is more robust than an index based on a single survey. Nonetheless, the summer-only indices were adequate, as they produced the same general patterns, with statistical significance, as the spring+summer indices. An increase in the number of years from eight (1998-2005) to eleven (1995-2005) increased statistical power even with a 35% drop in N site-pairs, but adding three more years (1992-2005) dropped N site-pairs another 57% and statistical power was about equal to the 1998-2005 dataset, which had an N 3.5 times as high. This shows the importance of having both enough sites and enough years to obtain statistical power, because butterfly populations are among the most highly variable of organisms studied (Gibbs et al. 1998). Since Karner blues exhibit such great annual fluctuation (literature cited above), adding more monitoring years should be disproportionately valuable compared to less variable species, because extreme fluctuations provide much of the amplitude for analyses of population synchrony. Increasing the number of years is the most important way to increase statistical power for detecting bird population trends (Cox 1990). The 1992-2005 period was the only one where our sample was <15 sites; in an IBD review of gene flow in insects, Peterson and Denno (1998) found that studies with at least 15 sites had twice the probability of detecting significant effects as those with <15.

CONCLUSION

Karner blues have a very high background rate of regional spatial autocorrelation, presumably due to environmental factors (relatively uniform and continental climate throughout Wisconsin range). This large regional spatial autocorrelation increases risk of synchronized extirpation (Harrison and Quinn 1989, Koenig 2001), especially in small or highly variable populations (Pollard and Yates 1992). This extinction risk is exacerbated by the tendency of major human-caused disturbance patterns to be spatially autocorrelated (Kallimanis et al. 2005). Weather and low fluctuations have been implicated in extirpations or sharp declines of Karner blues, including sites with formerly high populations (Packer 1994, Schweitzer 1994, Labus et al. 2002). The Karner blue recovery plan (U.S. Fish and Wildlife Service 2003) is built around management of metapopulations. If Karner blues are in metapopulations, then

correlations in their abundance are likely to decline rapidly beyond a certain short distance over which butterfly genetic exchange occurs. Our results support this view of Karner blue population structure, because strong local synchrony above regional background levels occurred at short distances (<3 km). Another assumption of metapopulation theory is that there is a rescue (reinforcing) effect of proximate demes, but synchrony of local population fluctuations makes rescue less likely in low years.

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