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Koenig, W D

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Spatial Synchrony of Monarch Butterflies

WALTER D. KOENIG¹

Hastings Reservation, University of California Berkeley, Carmel Valley 93924

ABSTRACT.—I examined spatial synchrony in populations of monarch butterflies (*Danaus plexippus*) during the summer breeding season across North America and while overwintering along the Pacific Coast. Spatial synchrony was observed in all analyses, but was particularly great among eastern summer populations and among overwintering populations on the Pacific Coast. Thus, in a year when relatively large numbers of monarchs were found at a particular breeding or wintering site in these populations, other sites within a wide area were likely to have relatively large numbers of monarchs as well. Spatial structure, measured by the decline in synchrony with distance, was relatively strong among summer populations in eastern North America, weaker, but present, among western summering populations and virtually nonexistent among overwintering populations along the Pacific Coast. Spatial synchrony in mean temperatures during the relevant time periods was generally much greater than that observed in the monarchs, consistent with the hypothesis that environmental factors (the Moran effect) may be playing a central role in causing the observed population synchrony. However, differences in spatial structure between monarch populations and mean temperature during the summer suggest that other factors, possibly post-migratory dispersal, are also affecting synchrony. Dispersal is particularly likely to be important in determining the unusual lack of spatial structure observed in overwintering populations of monarchs, which are believed to mix over wide areas during fall migration.

INTRODUCTION

Populations frequently vary in abundance more or less in unison over considerable geographic distances. Such spatial synchrony is of considerable interest and has motivated a large number of population studies (Bjørnstad *et al.*, 1999; Koenig, 1999). Causes of synchronous population fluctuations have been generally attributed to one or more of three broadly defined processes: dispersal, regional environmental synchrony (the Moran effect) and synchronous trophic effects (Liebhold *et al.*, 2004).

Beyond the causes, the magnitude and geographic extent of synchrony is of interest for at least two reasons. First, these population characteristics influence the likelihood of both local extinction and of population rescue, factors central to metapopulation dynamics (Brown and Kodric-Brown, 1977; Harrison and Quinn, 1989; Stacey and Taper, 1992; Hanski, 1998). Second, spatial synchrony reveals information of value for population monitoring. Specifically, if a species exhibits low spatial synchrony, size of any particular local population may not reflect trends in populations even a short distance away. In contrast, if spatial synchrony is high and its geographic extent great, the population size of any one population will generally correlate well with other populations, even those far away (Koenig, 2001).

Determining the degree, extent and causes of spatial synchrony are, thus, of importance to both the population ecology and conservation of natural populations. Here I discuss these phenomena in monarch butterflies (*Danaus plexippus*) at both of the two major periods of their multi-generational annual cycle: during their breeding season in the summer and, several generations later following migration, while overwintering in the fall.

¹ e-mail: koenigwd@berkeley.edu

Monarchs are widespread butterflies in North America, where there are two geographically distinct populations. Those breeding east of the Rocky Mountains (roughly about 105°W longitude) migrate primarily to overwintering sites in central Mexico, whereas those breeding west of the Rockies overwinter in forest stands along the Pacific coast (Malcolm, 1987; Lane, 1993; Malcolm and Zalucki, 1993; Swengel, 1995). Both form overwintering aggregations that can number in the tens of thousands on the Pacific Coast and upwards of hundreds of millions in the transvolcanic mountains west of Mexico City (Brower *et al.*, 2002). These large aggregations and, thus, significant fractions of the population are relatively vulnerable to environmental catastrophes (Brower *et al.*, 2004) and human disturbance, rendering classification of monarch migration and overwintering as a “threatened phenomenon” by the IUCN—World Conservation Union (New, 1993).

Swengel (1995) examined population fluctuations in monarchs based on surveys conducted over an 18-y period during the summer and found considerable annual variation related in part to environmental factors along with evidence for some degree of synchrony between the Atlantic and Midwestern subregions. Although not analyzed in detail from the perspective of spatial synchrony, her results add to a considerable literature examining population fluctuations in breeding populations of butterflies, including several comparative studies specifically focusing on spatial patterns (Pollard, 1991; Hanski and Woiwod, 1993; Raimondo *et al.*, 2004). In contrast, no prior study focusing specifically on spatial synchrony has been performed on a wintering population of butterflies, nor has a comparison of breeding and overwintering populations of the same species been performed. Such analyses are uniquely possible for monarchs as a consequence of surveys conducted since 1977 during the summer throughout North America (Swengel, 1990, 1995) and along the Pacific Coast at overwintering sites since 1997 near the end of November (Frey and Schaffner, 2004; Frey *et al.*, 2004).

Using results from these two monitoring programs, the primary goal of this study was to analyze and compare patterns of spatial synchrony found in breeding vs. wintering populations of monarchs. In addition, I compared the observed patterns of synchrony with that of mean temperature in an attempt to assess the importance of environmental factors compared to dispersal as causes of the observed spatial synchrony.

METHODS

MONARCH SURVEYS

The analyses conducted here are based on two independent sets of surveys. The first, started by the Xerces Society in 1975 and currently administered by the North American Butterfly Association (www.naba.org), is known as the 4th of July Butterfly Count (4JC). This count surveys North American butterflies in general, including breeding populations of monarchs (Swengel, 1990, 1995). Surveys are modeled after the better-known Christmas Bird Counts run by the National Audubon Society (Koenig, 2001) and consist of a variable number of observers surveying butterflies within a 24-km diameter count area during a period of one day during the summer, usually between mid-June to late July, each year. Values reported include the number of monarchs seen and the number of party hours, a measure of survey effort. Data from 396 count areas across the U.S. and southern Canada conducted between 1977 and 1999 were available in digitized form for analysis (Fig. 1). Sites were divided at 105°W longitude into western 4JC sites, which include populations that winter primarily along the Pacific Coast, and eastern 4JC sites, which encompass populations wintering mostly in Mexico. Not all areas were surveyed each year. Sites ranged between <50 km and up to 2421 km (western) and 3741 km (eastern) apart.

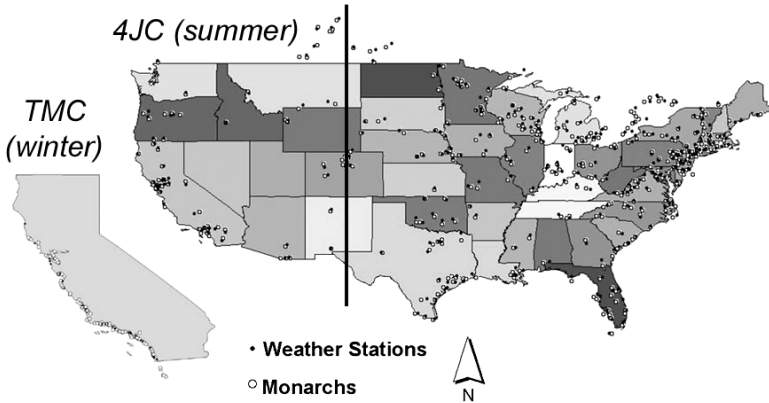


FIG. 1.—Geographic distribution of the Thanksgiving Monarch Counts (TMC; map of California on the left) and 4th of July Butterfly Counts (4JC; map of US on the right); the dark vertical line in the latter map marks the division between eastern and western populations (105° longitude) used in the analyses. In both cases, sites where monarchs were surveyed and sites from which temperature data were obtained are plotted

The second set of surveys, known as Thanksgiving Monarch Counts (TMC), initiated in 1997 by the Monarch Program and more recently coordinated by the Xerces Society (<http://www.xerces.org/home.htm>), is designed to monitor overwintering populations along the Pacific Coast. Surveys consist of estimating the total number of monarchs present at specific sites on an arbitrarily chosen day on or about the fourth Thursday in November (American Thanksgiving), relatively soon after monarchs arrive at their wintering sites. Data from 187 specific sites between Mendocino County, California and northern Baja California surveyed between 1997 and 2003 were analyzed (Fig. 1). As with the 4JC surveys, not all areas were surveyed each year. Intersite distances ranged up to 985 km apart.

TMC observers are generally experienced biologists or volunteers and undergo training to facilitate estimation of numbers. This is less true of the 4JC, which are mostly conducted by volunteers with little or no formal training. Thus, as is true with Christmas Bird Counts (Bock and Root, 1981; Swengel, 1990), estimates are subject to a variety of biases and problems. Furthermore, the differing methodologies of the two surveys and population structure of monarchs during the two seasons (highly aggregated in the winter but not in the summer) mean that values from the two sets of surveys are not directly comparable. Otherwise, these problems are generally expected to increase count variability and hence decrease the overall extent of spatial synchrony observed in the data. Thus, the observed levels of spatial synchrony are quite possibly underestimates of the actual values.

A summary of the number of counts and mean number of monarchs counted (in the case of 4JCs standardized for effort by dividing by party hours) are listed in Table 1. For 4JCs, sites not reporting party hours and those conducted in Mexico were excluded, while for both 4JC and TMCs only sites surveyed for a minimum of three years were included in the analyses. Left were a total of 2827 site \times year 4JC surveys and 747 site \times year TMC surveys. For 4JCs, an average of 123 sites (17 to 304) was surveyed each year with a mean of 7.2 years per site. For TMCs, an average of 107 sites (range 89 to 122) was surveyed each year with a mean of 5.2 y per site.

TABLE 1.—Number of sites and mean (\pm SE) number of monarchs counted per site during the study

Year	N summer sites surveyed	Mean \pm SE monarchs per party hour	N winter sites surveyed	Mean \pm SE monarchs per site
1977	18	0.73 \pm 0.23	—	—
1978	17	1.02 \pm 0.46	—	—
1979	30	0.57 \pm 0.18	—	—
1980	36	0.35 \pm 0.11	—	—
1981	33	0.81 \pm 0.25	—	—
1982	34	0.76 \pm 0.30	—	—
1983	27	0.29 \pm 0.10	—	—
1984	42	0.78 \pm 0.28	—	—
1985	39	1.53 \pm 0.48	—	—
1986	57	0.91 \pm 0.19	—	—
1987	74	0.89 \pm 0.20	—	—
1988	86	0.33 \pm 0.06	—	—
1989	102	0.94 \pm 0.16	—	—
1990	104	1.20 \pm 0.42	—	—
1991	138	2.51 \pm 0.53	—	—
1992	165	1.02 \pm 0.16	—	—
1993	188	0.78 \pm 0.10	—	—
1994	224	1.62 \pm 0.21	—	—
1995	261	0.62 \pm 0.06	—	—
1996	283	0.88 \pm 0.10	—	—
1997	304	1.99 \pm 0.18	93	12,228 \pm 2288
1998	289	0.72 \pm 0.10	103	5447 \pm 1470
1999	276	1.45 \pm 0.18	107	2315 \pm 675
2000	—	—	122	3089 \pm 690
2001	—	—	121	1706 \pm 456
2002	—	—	89	1090 \pm 379
2003	—	—	112	1951 \pm 504

Raw annual means for both surveys exhibited significant or nearly significant long-term trends, positive in the case of the 4JCs (linear regression of monarchs per party hour on year; standardized $\beta = 0.05$, $F_{1,2825} = 8.2$, $P < 0.01$) and negative in the case of the TMCs (linear regression of monarchs on year; standardized $\beta = -0.24$, $F_{1,745} = 43.9$, $P < 0.001$). In order to minimize the effects of these long-term global trends and focus on the short-term, year-to-year differences of interest here, all analyses were conducted on detrended values using the residuals from linear regressions of the number of monarchs counted (per party hour in the case of the 4JCs) on year within each site.

SPATIAL SYNCHRONY

Patterns of spatial synchrony were determined by means of the modified correlogram technique of Koenig and Knops (1998). In brief, distance between sampling sites and Pearson correlations between monarch numbers counted at these locations were calculated between all pairwise sets of sites using all years for which both sites were surveyed. Pairs of sites were then placed into one of six distance categories [≤ 50 km, >50 –100 km, >100 –250 km, >250 –500 km, >500 –1000 km, and (4JCs only) >1000 km] depending on the great-circle distance between them; I used distance categories that were the same for all analyses in

order to facilitate comparisons. I then calculated the mean correlation coefficient and tested this value statistically using randomization trials on sets of correlation coefficients from combinations of sites located a given distance apart. For each distance category, 1000 trials were conducted. Significance values were based on 1-tailed tests, since it is unlikely that synchrony would increase with distance (Liebhold *et al.*, 2004). All analyses were performed on data detrended within sites, as discussed above, in order to control for long-term global trends in population numbers occurring during the length of the study. Mantel tests (Manly, 1986) were performed on the sets of correlations in order to test for the presence of an overall relationship between synchrony and distance (spatial structure) in the data. Mantel tests yield two statistics, both of which theoretically vary from -1 to 1 : the standardized Mantel z value, which is a modified correlation coefficient measuring the strength and direction of the relationship between synchrony and distance, and the slope of $\log(\text{distance})$ on r (henceforth referred to as the "slope"), which measures the rate at which synchrony declines with distance. In order to facilitate comparisons between the two surveys, I performed Mantel tests not only using all 4JC data, but also excluding sites >985 km apart, the maximum intersite distance in the TMC surveys.

In order to determine whether observed patterns of spatial synchrony in monarch populations could be caused by the Moran effect, I compared spatial synchrony in the monarchs to mean temperature during the period most likely to be affecting the target populations. In the case of the 4JCs, exact timing varies considerably with latitude, but populations generally return to their summering areas by May and surveys were most frequently conducted in early July. Thus, I used mean temperature for the month of June as being the most likely to represent conditions affecting the populations of monarchs surveyed by the 4JCs. In the case of the TMCs, mean November temperature was chosen because this was the month encompassing the period when the majority of monarchs arrive at and, thus, presumably choose overwintering sites (Frey *et al.*, 2004). Analyses were also performed using June and November rainfall, but results were similar and are not presented here.

Monthly weather data, obtained from the National Climate Data Center online web site (<http://www.ncdc.noaa.gov/oa/ncdc.html>), was matched as closely as possible to the sites at which monarchs were surveyed. On average, the distance between 4JC monarch survey sites and sites at which mean summer temperatures were taken was 24.4 km. Mean summer temperature was available for 41% of all 4JC annual surveys.

For the TMCs, I used weather data from all available coastal California sites between Fort Bragg and San Diego, essentially the same range that the monarch surveys were conducted. Survey and weather station sites used for both sets of analyses are plotted in Figure 1.

As with the monarch data, I calculated modified correlograms and performed Mantel tests to examine spatial structure. In order to match the monarch data, values were detrended and analyses were performed both using all data and only values for sites <985 km apart.

RESULTS

Mean number of monarchs counted per party hour during the 4JC surveys ranged up to 68.8, while the maximum estimated number of monarchs overwintering at an individual site along the Pacific Coast was 120,000. Mean values of both varied considerably among years. The highest mean values were counted in 1991 (4JC) and 1997 (TMC), while the lowest were in 1983 (4JC) and 2002 (TMC) (Table 1). Unfortunately, with only three years encompassed by both surveys, it was not possible to compare trends between the two datasets during the same time period. The declining trend evident in the TMC was hypothesized by

Frey *et al.* (2004) to be due to increasingly severe drought conditions in the western U.S., particularly since the El Niño year of 1998.

For the eastern 4JCs and TMCs, monarch populations exhibited extensive spatial synchrony that was statistically significant ($P < 0.01$) between sites up to 1000 km apart, the farthest distance category for the TMCs (Fig. 2, top and bottom panels). In contrast, spatial synchrony between western 4JC sites was significant only between sites up to 100 km apart, after which values dropped off quickly (Fig. 2, center). Absolute value of spatial synchrony in monarch populations was modest, in all cases < 0.4 , and was considerably lower than the degree of synchrony in the environmental data (Fig. 2).

Measures of spatial structure differed considerably among the data sets. Summer populations, both eastern and western, exhibited highly significant declines in synchrony with distance when considering all data, the slope being steeper in eastern than western North America (Table 2). When analyses were restricted to sites < 985 km apart, both measures of structure were reduced, but remained significant. In contrast, overwintering populations of monarchs exhibited no significant spatial structure, although the slope of $\log(\text{distance})$ on r was nearly identical to that exhibited by western summering populations restricted to sites < 985 km apart. The decline in synchrony in mean November temperature was also small, even less than that in the wintering monarch populations, although it was statistically significant.

DISCUSSION

Monarchs exhibit moderate ($r < 0.4$), statistically significant spatial synchrony over large distances (sites up to 1000 km apart) in eastern North America during the summer and along the Pacific Coast while overwintering (Fig. 2). Spatial synchrony was considerably lower, and significant only between sites up to 100 km apart, in western North America during the summer. Thus, spatial synchrony in general appears to be considerably greater among eastern summer populations and western overwintering populations than among western summer populations.

Synchrony in ecological phenomena often exhibit significant spatial structure in the form of a decline in synchrony with distance (Liebhold *et al.*, 2004). Such a decline was highly significant in eastern summer monarch populations, even when restricting analyses to the same range of intersite distances as present in the overwintering data. A decline in synchrony with distance was also observed in the western summer monarch data, but was considerably less and only marginally significant when restricted to sites < 985 km apart. No significant evidence of spatial structure was detectable in the overwintering populations; that is, synchrony was equally strong between sites far apart as between those close together. Thus, a large number of monarchs at an individual site along the Pacific Coast is generally likely to indicate relatively large numbers elsewhere, even at sites hundreds of km away.

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FIG. 2.—Spatial synchrony in monarch butterflies and environmental conditions throughout the U.S. during summer 1977–1996 (top; based on 4th of July monarch counts) and in coastal California during fall 1997–2003 (bottom; based on Thanksgiving monarch surveys). Values graphed are the mean correlation between pairwise sites grouped into 6 distance categories (no sites were > 1000 km apart in the winter surveys). Solid symbols are values significantly greater than zero at the $P < 0.05$ level. Environmental conditions are mean average temperature for the month of June (top) and month of November (bottom). All values detrended to remove long-term trends. Sites are mapped in Figure 1

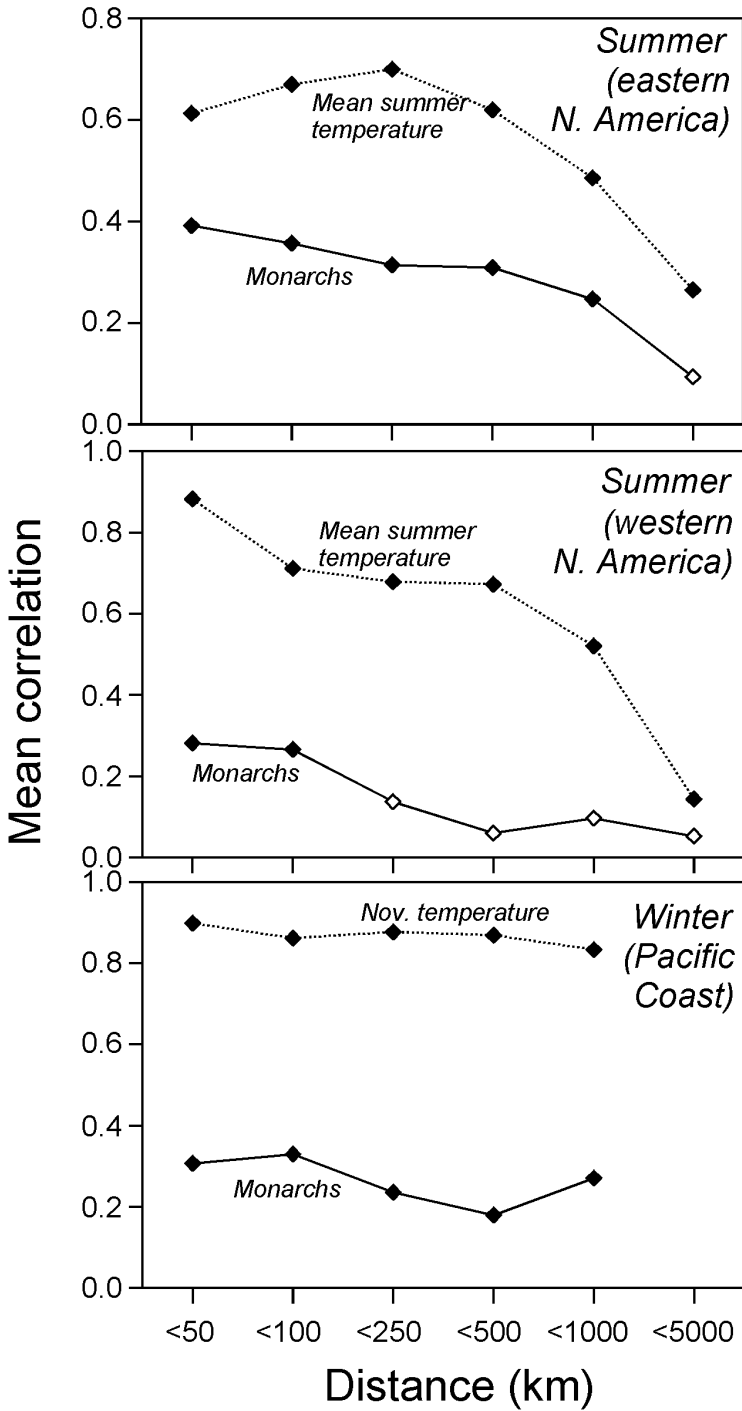


TABLE 2.—Mantel tests for spatial structuring of wintering monarch populations and coastal California weather conditions, 1997–2003, and in summering monarch populations and mean June temperature at matched sites, 1977–1999. Summer populations are divided at 105°W longitude and include all sites and only intersite comparisons <985 km apart. All analyses performed on detrended values in order to remove long-term trends in the data. N = number of site × years included in the analysis; significance (1-tailed) based on randomization tests

Variable	N sites	Slope of log(distance) on r	Mantel z	P-value
Summer—eastern N. America (all data)				
Monarchs	327	−0.110	−0.171	<0.001
Mean June temperature	145	−0.176	−0.255	<0.001
Summer—western N. America (all data)				
Monarchs	69	−0.039	−0.111	<0.001
Mean June temperature	36	−0.196	−0.456	<0.001
Summer—eastern N. America (<985 km only)				
Monarchs	327	−0.038	−0.066	<0.001
Mean June temperature	145	−0.063	−0.143	<0.001
Summer—western N. America (<985 km only)				
Monarchs	69	−0.023	−0.070	<0.05
Mean June temperature	36	−0.124	−0.308	<0.001
Fall—Pacific Coast				
Monarchs	144	−0.020	−0.006	ns
Mean November temperature	23	−0.013	−0.142	<0.02

Spatial synchrony has previously been detected in breeding populations of other Lepidoptera species, but not on a geographic scale anywhere as large as detected here (Pollard, 1991; Sutcliffe *et al.*, 1996; Raimondo *et al.*, 2004).

Of the three primary mechanisms by which spatial synchrony on the scale observed here can be generated, trophic effects are unlikely to play a significant role in synchronizing monarch populations given that they are poisonous and subject to relatively little systematic predation. In contrast, both dispersal or dependence on regionally correlated environmental factors (the Moran effect; Ranta *et al.*, 1997; Liebhold *et al.*, 2004) could be playing important synchronizing roles. The Moran effect is almost always potentially important, since major weather factors such as temperature and rainfall are universally synchronous over large geographic areas (Koenig, 2002). To the extent that the Moran effect is driving spatial synchrony in monarchs, synchrony in environmental factors should be at least as great as that observed in the monarchs and should exhibit similar relationships between synchrony and distance.

In general, the first of these conditions was met in the data analyzed here: spatial synchrony in environmental conditions (mean temperature) during the appropriate month was considerably higher than that observed in the monarchs (Fig. 2). As for pattern, the best comparative measure is provided by the slope of log(distance) on r. Comparing these values, the decline in synchrony was considerably greater for mean June temperature than in monarchs for both western and eastern populations, with the slope of log(distance) on r for the monarchs being about 60% of the slope of log(distance) on r for mean June temperature in eastern North America, and only 20% of the slope of log(distance) on r for mean June temperature in western North America (Table 2). In contrast, the decline in

synchrony of mean November temperature along the Pacific Coast was small (although statistically significant), even less than the nonsignificant decline in synchrony observed in overwintering monarchs.

The generally higher spatial synchrony observed in mean temperatures compared to monarchs suggests that, as in other butterfly populations (Pollard, 1988, 1991; Sutcliffe *et al.*, 1996; Raimondo *et al.*, 2004), the Moran effect is probably playing an important role in influencing the observed synchrony in monarch populations. However, the much stronger decline in synchrony with distance observed in June temperatures compared to monarch populations suggests that other factors may also be important, either by decreasing synchrony between sites relatively close together or increasing synchrony between sites far apart, relative to that expected based solely on environmental conditions. A likely candidate for such a factor is long-distance, post-migratory movements during the summer unrelated to environmental conditions.

Although not directly tested by the analyses performed here, dispersal is also likely to play a role in synchronizing and reducing the observed degree of spatial structure in overwintering populations of monarchs. There are at least two ways that this could be occurring. First is dispersal among overwintering sites shortly after arrival. Based on three years of tagging, Frey *et al.* (2004) found little evidence that monarchs, once settled into a site, moved further than 15 km, and none was observed to move between any of the counties covered by their surveys. Consequently, dispersal among sites after arrival on the Pacific Coast is unlikely to be driving synchrony except over very short distances.

The second potentially important form of dispersal is mixing during the fall migration itself. Tagging efforts in the western U.S., although limited, support the hypothesis that such mixing is widespread and thus may play an important role in the observed lack of spatial structure among overwintering populations (Urquhart and Urquhart, 1977; Marriott, 2001). For example, individuals marked during summer 1976 in Boise, Idaho were later found over a 400 km stretch of the California coast between Santa Cruz and Santa Barbara, while animals marked inland at Salem, Oregon were later found across 660 km of coast between Reedsport, OR and Bolinas, CA (Urquhart and Urquhart, 1977). Assuming individuals settle within a relatively short distance of where they eventually reach the coastline, as indicated by the work of Frey *et al.* (2004), such apparently extensive mixing during the autumnal migration could obliterate any spatial structure that might otherwise be expected within the 1000 km range covered by the overwintering data.

In contrast to the lack of spatial structure observed in overwintering populations of monarchs, virtually all summer Lepidopteran populations that have been analyzed to date, including the eastern North American populations of monarchs analyzed here, exhibit significant declines in synchrony with distance, often over relatively small areas (Sutcliffe *et al.*, 1996; Raimondo *et al.*, 2004; Satake *et al.*, 2004). Sutcliffe *et al.* (1996), for example, examined butterfly species in the U.K. and found significant declines in synchrony over distances of only 1–2 km. At larger, regional scales, populations remained partially synchronized over distances of 200 km, but synchrony still declined with distance. These authors found species mobility to play a minor role maintaining synchrony at a regional level and, thus, concluded that environmental factors are primarily responsible for the observed synchrony. Similar conclusions were reached by Raimondo *et al.* (2004) for 10 species of Lepidoptera in the eastern U.S. Although the Moran effect may also be the critical factor determining synchrony in summering populations of monarchs, the extensive mixing that occurs during migration makes it likely that mobility is potentially playing a much more important role in driving the patterns observed in spatial synchrony of overwintering populations of monarchs. The main caveat to this conclusion is that both overwintering

monarchs and environmental conditions along the coast during the time that the monarchs arrive exhibit virtually no decline in synchrony with distance. Thus, it is not possible to reject the hypothesis that the pattern of spatial synchrony in overwintering monarchs is being driven in part by a similar pattern of spatial synchrony in environmental conditions.

These results have implications in terms of monitoring monarch populations during the summer and while wintering along the Pacific Coast. Most importantly, they suggest that, at least for summer populations in the eastern U.S. and overwintering populations along the Pacific Coast, monitoring a small number of sites may yield reasonably good estimates of the population numbers within a much larger area, since relatively large numbers of monarchs at such sites is likely to correlate with relatively large numbers at sites hundreds or even a thousand km away. This is particularly true for overwintering populations along the Pacific Coast, which exhibit virtually no decline in synchrony with distance. Nonetheless, although significant over a large geographic area, the fairly modest degree of synchrony observed in monarch populations still leaves room for considerable local variation in numbers that only extensive and detailed surveys at local levels are likely to detect.

A corollary of the large-scale, significant spatial synchrony documented here is that the metapopulation phenomenon of population rescue (Brown and Kodric-Brown, 1977; Stacey and Taper, 1992) is unlikely to play an important role in maintaining local populations. Rather, local populations of monarchs can be expected to grow or go extinct synchronously as a consequence of climatic factors influencing survival and reproduction over large geographic scales. This highlights the importance of conservation efforts among areas where large numbers of monarchs congregate, such as in the winter along the Pacific Coast and particularly in the transvolcanic mountains west of Mexico City where hundreds of millions of animals overwinter (Brower *et al.*, 2002; Missrie, 2004).

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LITERATURE CITED

- BJØRNSTAD, O. N., R. A. IMS AND X. LAMBIN. 1999. Spatial population dynamics: analysing patterns and processes of population synchrony. *Trends Ecol. Evol.*, **14**:427–431.
- BOCK, C. E. AND T. L. ROOT. 1981. The Christmas Bird Count and avian ecology. *Stud. Avian Biol.*, **6**:17–23.
- BROWER, L., G. CASTILLEJA, A. PERALTA, J. LOPEZ-GARCIA, L. BOJORQUEZ-TAPIA, S. DIAZ, D. MELGAREJO AND M. MISSRIE. 2002. Quantitative changes in forest quality in a principal overwintering area of the monarch butterfly in Mexico, 1971–1999. *Conserv. Biol.*, **16**:346–359.
- BROWER, L. P., D. R. KUST, E. RENDON SALINAS, E. GARCIA-SERRANO, K. R. KUST, J. MILLER, C. FERNANDEZ DEL RAY AND K. PAPEW. 2004. Catastrophic winter storm mortality of monarch butterflies in Mexico during January 2002. *In*: K. S. Oberhauser and M. J. Solensky (eds.). *The monarch butterfly: biology and conservation*. Cornell University Press, Ithaca, New York.
- BROWN, J. H. AND A. KODRIC-BROWN. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**:445–449.
- FREY, D. AND A. SCHAFFNER. 2004. Spatial and temporal pattern of monarch overwintering abundance in western North America. *In*: K. S. Oberhauser and M. J. Solensky (eds.). *The monarch butterfly: biology and conservation*. Cornell University Press, Ithaca, New York.
- , S. STEVENS, S. L. STOCK, J. L. GRIFFITHS AND J. SCOTT. 2004. Monarch butterfly population dynamics in Western North America—emphasis on Monterey and San Luis Obispo counties,

- winter 2003–2004 report. California Polytechnic State University and Ventana Wilderness Society. 1–63 p.
- HANSKI, I. 1998. Metapopulation dynamics. *Nature*, **396**:41–49.
- AND I. P. WOIWOD. 1993. Spatial synchrony in the dynamics of moth and aphid populations. *J. Anim. Ecol.*, **62**:656–668.
- HARRISON, S. AND J. F. QUINN. 1989. Correlated environments and the persistence of metapopulations. *Oikos*, **56**:293–298.
- KOENIG, W. D. 1999. Spatial autocorrelation of ecological phenomena. *Trends Ecol. Evol.*, **14**:22–26.
- . 2001. Spatial autocorrelation and local disappearances in wintering North American birds. *Ecology*, **82**:2636–2644.
- . 2002. Global patterns of environmental synchrony and the Moran effect. *Ecography*, **25**:283–288.
- AND J. M. H. KNOPS. 1998. Testing for spatial autocorrelation in ecological studies. *Ecography*, **21**:423–429.
- LANE, J. 1993. Overwintering monarch butterflies in California: past and present. In: S. B. Malcolm and M. P. Zalucki (eds.). *Biology and conservation of the monarch butterfly*. Natural History Museum of Los Angeles, Los Angeles.
- LIEBHOLD, A., W. D. KOENIG AND O. N. BJØRNSTAD. 2004. Spatial synchrony in population dynamics. *Annu. Rev. Ecol. Evol. Syst.*, **35**:467–490.
- MALCOLM, S. B. 1987. Monarch butterfly migration in North America: controversy and conservation. *Trends Ecol. Evol.*, **2**:135–138.
- AND M. P. ZALUCKI (eds.). 1993. *Biology and conservation of the monarch butterfly*. Los Angeles County Museum of Natural History, Los Angeles, California. 419 p.
- MANLY, B. F. J. 1986. Randomization and regression methods for testing for associations with geographical, environmental and biological distances between populations. *Res. Popul. Ecol.*, **28**:201–218.
- MARRIOTT, D. F. 2001. Mapping autumnal movements. *Monarch Quarterly*, **11**(2):9–12.
- MISSRIE, M. 2004. Design and implementation of a new protected area for overwintering monarch butterflies in Mexico. In: K. S. Oberhauser and M. J. Solensky (eds.). *The monarch butterfly: biology and conservation*. Cornell University Press. Ithaca, New York.
- NEW, T. R. (ed.). 1993. *Conservation biology of Lycaenidae (Butterflies)*. The World Conservation Union, Gland, Switzerland.
- POLLARD, E. 1988. Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**:819–828.
- . 1991. Synchrony of population fluctuations: the dominant influence of widespread factors on local butterfly populations. *Oikos*, **60**:7–10.
- RAIMONDO, S., A. M. LIEBHOLD, J. S. STRAZANAC AND L. BUTLER. 2004. Population synchrony within and among Lepidoptera species in relation to weather, phylogeny, and larval phenology. *Ecol. Entomol.*, **29**:96–105.
- RANTA, E., V. KAITALA, J. LINDSTRÖM AND E. HELLE. 1997. The Moran effect and synchrony in population dynamics. *Oikos*, **78**:136–142.
- SATAKE, A., O. N. BJØRNSTAD AND S. KOBRO. 2004. Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. *Oikos*, **104**:540–550.
- STACEY, P. B. AND M. TAPER. 1992. Environmental variation and the persistence of small populations. *Ecol. Appl.*, **2**:18–29.
- SUTCLIFFE, O., C. D. THOMAS AND D. MOSS. 1996. Spatial synchrony and asynchrony in butterfly population dynamics. *J. Anim. Ecol.*, **65**:85–95.
- SWENGEL, A. B. 1990. Monitoring butterfly populations using the Fourth of July butterfly count. *Am. Midl. Nat.*, **124**:395–406.
- . 1995. Population fluctuations of the Monarch (*Danaus plexippus*) in the 4th of July butterfly count 1977–1994. *Am. Midl. Nat.*, **134**:205–214.
- URQUHART, F. A. AND N. R. URQUHART. 1977. Overwintering areas and migratory routes of the monarch butterfly (*Danaus p. plexippus*, Lepidoptera: Danaidae) in North America, with special reference to the western populations. *Canadian Entomologist*, **109**:1583–1589.