Investigating Long-Term Changes in the Spring Migration of Monarch Butterflies (Lepidoptera: Nymphalidae) Using 18 Years of Data From Journey North, a Citizen Science Program

ELIZABETH HOWARD[1] AND ANDREW K. DAVIS[2,3]

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ABSTRACT Declines in overwintering colonies of monarch butterflies (*Danaus plexxipus*) in Mexico raise questions about other life cycle phases, such as spring migration, where monarchs recolonize their breeding range in the United States and Canada with sequential generations. We used data from a long-term citizen science program, "Journey North" (now with 18 yr), to identify possible changes to the recolonization. This program asks people to report the date and location when they see the first adult monarch annually, and this database now contains >11,000 records. We examined sighting dates and migration range size, the latter based on the number of 2-degree latitude–longitude grid squares with monarch sightings, to look for evidence of change in either of these two parameters over the 18 yr. Our analyses used regression models that accounted for increasing volunteer participation over the years. We found monarchs are being sighted later at a rate of 1 d later every 4 yr. This does not appear to be related to later emergence of milkweed, based on examination of milkweed reports. Later sightings could be interpreted as a sign of reductions in monarch abundance (it takes longer to see the first monarch of the year). We also found a potential decline in the geographic range of the initial spring migration wave (a decline of 9% over 18 yr). However we detected no change in the continental area encompassed at the end of recolonization, indicating monarchs are still successfully filling their traditional breeding range in eastern North America.

KEY WORDS monarch butterfly, *Danaus plexippus*, Danainae, spring migration, Journey North

Each fall in eastern North America, millions of monarchs travel 3,000+ kilometers to a select few mountaintop sites in central Mexico, where they spend the winter before travelling north in the spring to lay eggs and repopulate their breeding range. The pattern of repopulation, or recolonization, involves successive broods that progress northward so that the final stage of the spring migration is accomplished by monarchs that are two to three generations removed from the overwintering cohort (Cockrell et al. 1993). Importantly, in the past 20 yr, the size of the overwintering population has diminished significantly (Brower et al. 2012, Vidal and Rendon-Salinas 2014), and these declines engender questions regarding their effects on spring migration, which in theory should hinge upon the size of the returning migrant population each year. Specifically, if the number of monarchs overwintering in Mexico is diminishing over time, how will this change the spring migration? This is the primary question we address in the current paper.

There are a wide variety of citizen science projects devoted to monarchs (reviewed in Ries and Oberhauser 2015), but one of the longest running in North America is "Journey North" (http://www.learner.org/jnorth/). Since 1997, this program has asked its volunteers to report sightings of the first monarch each spring (along with other natural history phenomena), and these sightings are compiled in online maps (see Fig. 1), which are effective at documenting the progression of the returning migrants. While originally used as a classroom resource, this program has grown substantially, and the data have been extremely valuable to science, because of the program's continent-wide army (Howard and Davis 2004, 2011; Davis and Howard 2005). In fact, this is the only data series that allows for large-scale research into the spring migration of monarchs.

In prior work using the first 6 yr of Journey North sightings, we have identified the general route, or flyway, taken by returning migrants as they progress northward through the United States and Canada (Howard and Davis 2004). This effort showed how the migration wave first advances through Texas, then expands eastward through the southern and southeastern states, before advancing northward into the Midwest. Other work (also using data from the early years of program) showed a noticeable change in timing of sightings by the end of April, which marks the expiration of the overwintering generation, and the growth of the first spring generation (Davis and Howard 2005). Knowing this time point, we can then consider sightings prior to this to reflect the migration of returning

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[1] Journey North, Norwich, VT 05055.

[2] Odum School of Ecology, University of Georgia, Athens, GA 30602.

[3] Corresponding author, e-mail: akdavis@uga.edu.

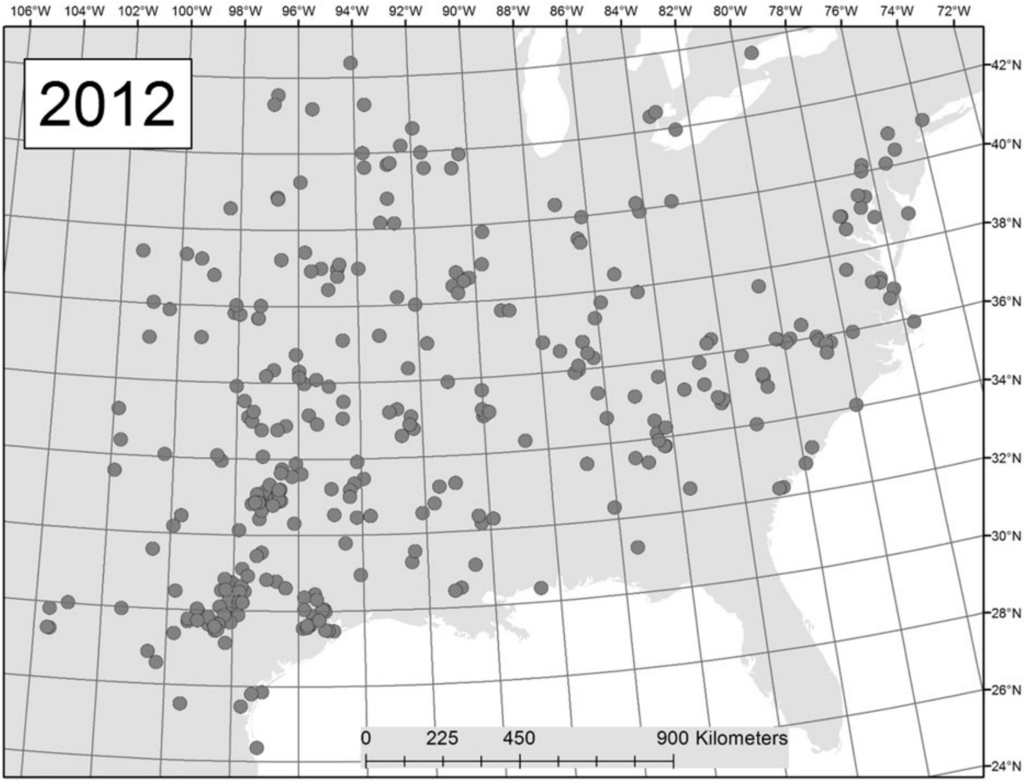

Fig. 1. Map of the early spring migration in the United States for a selected year (2012), as reported by Journey North participants. Shown are all first sightings of adult monarchs up until 30 April, which largely reflects the return of the overwintering generation. Note that in this year the early monarch recolonization was exceptionally successful. Sightings from Florida were not included here. The overlaid grid is shown to depict the 2° × 2° grid squares, or blocks used in analyses of migration wave size. Each grid is ~50,000 km^2.

adults, which should be closely tied to the size of the overwintering population. All sightings thereafter would reflect the reproductive success of the year.

The Journey North data set on spring migration now spans 18 yr ($n = 11{,}204$ records of monarchs east of the Rockies), and we note these years are concurrent with the major declines seen in overwintering population size (Brower et al. 2012, Vidal and Rendon-Salinas 2014). Here, we examined this data set to look for evidence of change in the timing of sightings or shrinking range size of the migration wave (both the returning adult cohort and the subsequent generations), which would be expected if the wintering population was declining. Results from this work will be valuable for comparison with other long-term data sets on monarch abundance or distribution and that focus on other periods of their life cycle.

Materials and Methods

Monarch Sightings. Journey North contributors are members of the public from all walks of life, including nature-centered volunteers, interested citizens, and elementary school children (Howard and Davis 2004). The rules of the program are simple: the participants report (in an online portal) the day and location where and when they spotted the first adult monarch of the year, while they were going about their daily activities. They are encouraged to provide notes about the sighting, which help to verify the report, although it is not required. If a report is questionable, the Journey North staff attempt to verify the sighting with the observer by further inquiry. Then, the staff compiles and posts all confirmed sightings to an online map, which depicts the progress of the spring migration. As an example of this, we have plotted sightings from 1 yr (2012) up to the end of April (Fig. 1). All sightings consist of at least the date, the town where the observer lives (or where the sighting took place), the US state or Canadian province, and the latitude and longitude (which are filled in by staff if not provided). Note that the sightings database consists of reports from both east and west of the Rocky Mountains, but for the purposes of this study, we only focused on eastern sightings, as monarchs in this population make up the vast majority of the overwintering cohort in Mexico. It is also important to point out that participation in this program has steadily risen over the years (Howard and Davis 2011), which needs to be accounted for in most analyses of these data (below).

Data Analyses. The first element of the migration we examined was the timing of the spring migration over the 18-yr period. Here we were interested in identifying any temporal changes that may have occurred throughout the spring migration (i.e., over the entire range), and so we used the entire data set ($n = 11{,}204$ records of monarchs east of the Rockies). First we converted the date of all monarch sightings into Julian date (number of days since 1 January), which we used as the response variable. This variable was normally distributed, based on visual inspection of its histogram. Then, we used multiple regression to examine three potential predictors of sighting date, which were all continuous variables. These were 1) the latitude associated with the sighting, since by default, sightings become later as the migration proceeds northward, 2) the number of sightings per year, which attempts to account for the increasing participation in the program, and 3) the year of sighting, which would determine if the timing of sightings has changed over the course of this program (18 yr).

Based partly on results from the analysis above, we further examined if milkweed emergence dates have changed over the time frame of this project. Journey North began soliciting this information from volunteers in 2001, and simply asks people to report the date they see the first milkweed leaves. We downloaded all records of milkweed emergence dates between March and May for the years 2001–2004 ($n = 654$), plus for the years 2011–2014 ($n = 1{,}546$). We did not include records from western states, nor any records from Florida, as milkweed grows year-round there. We then compared the average dates of milkweed emergence between the first time period (2001–2004) to the last (2011–2014) using a Student's t-test.

Next we considered possible changes to the spatial extent, or range size, of the spring migration wave (i.e. how much land it encompasses), which logically should approximate the size of the returning spring population (Howard and Davis 2011). For this we established a nominal grid over the spring flyway region, where each grid square was 2° latitude by 2° longitude (equivalent to ~50,000 km^2; Fig. 1). Next, we coded each monarch sighting according to what grid square it was in. Note that sightings in Florida were not included. This allowed us to tally how many grid squares contained monarchs for each year, which should closely approximate the overall size (spatial extent) of the migration. In particular, we tallied both the total number of grid squares per year (i.e. using all sightings from March through July), as well as only those sightings up to the end of April. This was so that we could compare the range size of the early migration wave against the final migration. The early wave would be primarily composed of returning adult monarchs from the overwintering sites in Mexico, and we were especially interested in knowing if this wave size has gotten smaller over time, as the overwintering colonies have declined over time (Brower et al. 2012, Vidal and Rendon-Salinas 2014).

The final data for this analysis were two sequences of values ($n = 18$ for each), with one showing the number of grid squares occupied each year prior to 30 April and one for the entire migration through to the end of July. These data were normally distributed, based on Shapiro–Wilk tests ($W = 0.95$, $P = 0.475$, and $W = 0.93$, $P = 0.229$). Then, we used multiple regression to search for linear relationships between these two variables (tested separately) and three key predictors: 1) the annual number of sightings for each time period (i.e. up to the end of April or the end of July), to control for varying participation, 2) the size of the overwintering colonies in Mexico, which we obtained from published sources (Brower et al. 2012, Vidal and Rendon-Salinas 2014) for the years that overlapped with our program (1997–2014), and 3) the effect of year (as a continuous variable), which would determine if there has been any directional change in the size of the migration wave(s) over the 18 yr. We did not incorporate timing of milkweed emergence, which varies from year to year (E. Howard, unpublished data), as these values (mean plant emergence dates per year) were highly correlated with the number of sightings, so that their inclusion did not improve the models of migration range size. All statistical tests in this paper were performed using the STATISTICA 12.1 software package (StatSoft, Tulsa, USA).

Results

Our analysis of the timing of monarch sightings indicated there have been significant changes in this parameter over the 18-yr program. The linear regression model of Julian date revealed a significant effect of year ($P < 0.0001$, $\beta = 0.25$; Table 1), after accounting for the effects of latitude ($P < 0.0001$, $\beta = 0.76$) and the number of observers (sightings) per season ($P < 0.0001$, $\beta = -0.12$). Because the direction of the year effect was positive, this indicates that monarch sightings are reported later with each passing year (roughly 1 d later every 4 yr). To help visualize this pattern, we plotted the average date of monarch sightings for all latitudes during the first 6 yr of the program, compared to the most recent 6 yr (Fig. 2). This figure shows that average sighting dates have shifted later across most latitudes along the flyway. The difference between time groups appeared to be largest at points below 30°N, or lower Texas, plus at latitudes 40 and 41, which is approximately midway through the United States.

The results above led us to examine if milkweed emergence dates have changed over time. Our comparison of average milkweed emergence dates between

Table 1. Summary of linear regression model that examined predictors of the date of adult monarch sighting (Julian day) across all 18 yr of data ($n = 11{,}204$)

Predictor[a]	df	t	P	Beta (SE)	Partial corr.[b]
No. of sightings/yr	1	−7.23	<0.00001	−0.12 (0.02)	−0.07
Latitude	1	130.77	<0.00001	0.76 (0.01)	0.78
Year	1	15.48	<0.00001	0.25 (0.02)	0.14

Overall test of model significance: $\text{df} = 11200$, $t = -15.78$, $P < 0.0001$, $R^2 = 0.62$.

[a] Intercept = −3607.6, SE = 228.7.

[b] Partial correlation (strength of the relationship between the predictor variable and the response variable, after controlling for all other independent variables in the model).

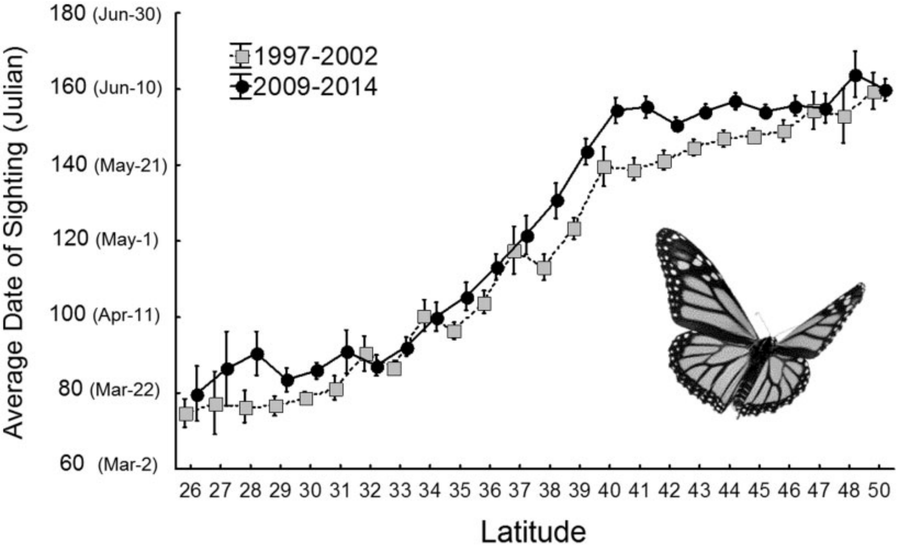

Fig. 2. Timing of monarch arrival to each latitude in the spring (Julian date) during the first 6 yr of the Journey North program (1997–2002; grey squares) and during the last 6 yr (2009–2014; black squares). Whiskers above and below means represent 95% confidence intervals. Note that latitude 49° is not shown due to low sample size, and all latitudes above 50° are pooled.

the earliest years for which data were available (2001–2004) and the latest years (2011–2014) indicated there was a significant difference (Student's t-test, df = 2,198, $t = 2.58$, $P = 0.0098$), but the average emergence date of the later years was earlier (by about 2 d) than it was in the first time period. Thus, we found no evidence that milkweed emergence is shifting later, as are the adult monarch sightings.

In our evaluation of long-term patterns in the spatial coverage of spring migration, we found the number of grid squares with monarch sightings was positively predicted by the number of sightings per year for both the early migration wave ($P < 0.001$, $\beta = 1.05$; Table 2) and the combined migration ($P = 0.003$, $\beta = 1.01$). Thus, the number of sightings per year appears to be a strong predictor of the spatial size of the migration wave. This pattern can be seen in a plot of both the number of sightings per year and the range size of the migration wave, for the period prior to 30 April (Fig. 3). The size of the overwintering colonies in Mexico did not appear to predict the geographic size of the migration wave, for both the early wave ($P = 0.651$, $\beta = -0.07$; Table 2), and the total migration ($P = 0.736$, $\beta = 0.05$). There was a nonsignificant negative relationship with year in the first model ($P = 0.089$, $\beta = -0.36$; Table 2), indicating that the range size of the returning wave is tending to decline with time. In contrast, there was absolutely no effect of year in the second model ($P = 0.810$, $\beta = -0.07$). Put another way, these results indicate the geographic size of the early spring migration wave has diminished slightly over the 18-yr period, but the spatial coverage of the entire migration wave has not.

Discussion

Our analyses of 18 yr of observations by Journey North participants show monarch spring migration patterns in eastern North America have changed in timing, with adult monarchs tending to be sighted later in more recent years. While we had no specific predictions regarding migration timing, this result was nevertheless interesting, because it seems counter to the fact that participation in this program has been increasing (Howard and Davis 2011); in other words, with more people looking for them, monarchs should be seen sooner rather than later. On the other hand, having more participants could mean that a greater number of late-migrating monarchs get sighted than would have in past years, which in theory could shift the average date of sightings back. Still another interpretation is that overall abundance of adult monarchs is declining during the spring (though the spatial area covered is not), which means that it takes longer for people to see their first monarch of the year. We do know that the delay in arrival timing of monarchs over time is not due to later emergence of milkweed in eastern North America. When we examined records of milkweed emergence we found no evidence milkweed is emerging later over time, which does not help to explain the later arrival time of monarchs. In fact, we found the opposite pattern, that emergence of milkweed is shifting earlier with time.

Our results concerning the geographic range of the spring migration may be more germane to monarch conservation. We detected a very slight (nonsignificant) decline in the range size of the returning migration wave, after accounting for increasing participation in the Journey North program (Table 2). Despite the fact that overwintering colony size did not predict the spatial size of spring migration in either of our models, the direction of this pattern at least is consistent with the long-term declines seen in the size of overwintering colonies in the last 20 yr (Brower et al. 2012, Vidal and Rendon-Salinas 2014). However, the magnitude of the

Table 2. Summary of two multiple regression models that examined key predictors of the migration wave size, either before 30 April (which captures the majority of returning adults), or for the entire spring migration

Response	Predictor	df	t	P	Beta (SE)	Partial Corr.[c]
No. of grid squares before 30 April[a]	Number sightings up to 30 April	1	6.97	<0.001	1.05 (0.15)	0.88
	Overwintering size	1	−0.46	0.651	−0.07 (0.16)	−0.12
	Year	1	−1.83	0.087	−0.36 (0.19)	−0.44
No. of grid squares for all migration[b]	Total number sightings	1	3.58	0.003	1.01 (0.28)	0.69
	Overwintering size	1	0.34	0.736	0.05 (0.14)	0.09
	Year	1	−0.24	0.810	−0.07 (0.30)	−0.06

The migration wave size was indexed by the number of 2° × 2° grid squares with monarch sightings in them (see Fig. 1), and the sample size for both models was 18. The number of sightings was included to account for the fact that participation in the Journey North program has steadily risen over time. Overall test of model significance for first model: df = 14, t = 1.86, P = 0.0834, R^2 = 0.89, and second model: df = 14, t = 0.28, P = 0.780, R^2 = 0.91.

[a] Intercept = 1880.3, SE = 1008.7.

[b] Intercept = 549.2, SE = 1929.2.

[c] Partial correlation (strength of the relationship between the predictor variable and the response variable, after controlling for all other independent variables in the model).

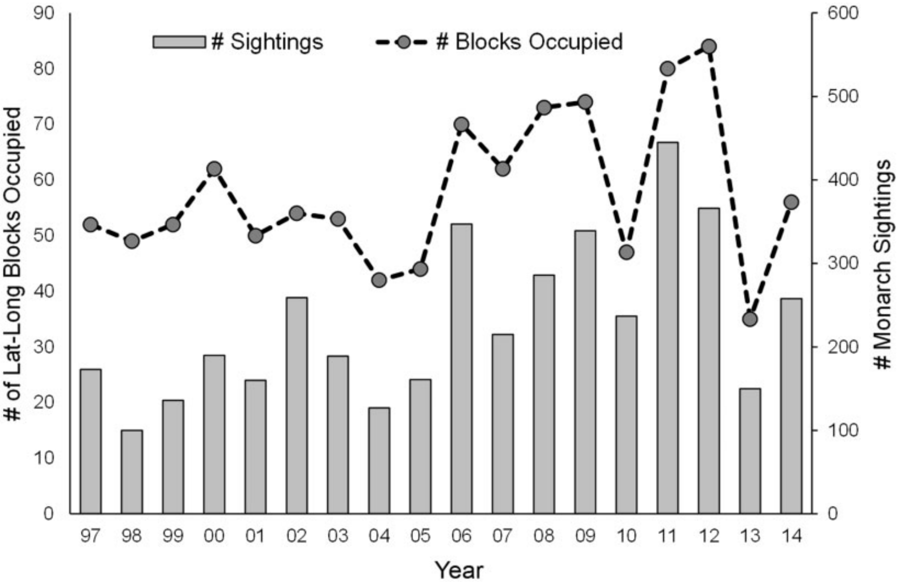

Fig. 3. Plot of the number of first monarch sightings reported to Journey North each year prior to April 30 (bars), overlaid with data on the range size of the returning migration wave (dotted line). The migration wave size was indexed by tallying the number of 2° × 2° latitude–longitude blocks containing monarch sightings (see Fig. 1). The take-home message from this is that the number of sightings per year is a key predictor of the range size of the migration wave each year, and therefore must be accounted for in analyses of this metric.

decline in our data certainly did not resemble the more dramatic decline (i.e. 90% drop over 20 yr) observed in overwintering colony size. Using the grid square system we employed here, the slope of decline (−0.36) suggests the spring migration wave is diminishing in geographic size by about 1 grid square (50,000 km^2) every 3 yr. For comparison, the average number of grid squares occupied by the end of April is 64.4 (14.38 SD), which is equivalent to 3.2 million km^2. By our calculations then, the area covered by the early migration wave is shrinking by ∼1.5% every 3 yr, or 9% over 18 yr.

In contrast to the results above, we detected absolutely no signal of change in the range size of the entire recolonization (Table 2), after accounting for varying participation in the program. This indicates that monarchs have still been able to colonize their full breeding range in eastern North America, despite the diminishing numbers in Mexico, and the shrinking early migration. This could be explained by the high reproductive capacity of monarchs; individual females can lay over 500 eggs (Svard and Wiklund 1988). It is also possible that the larvae produced by the earliest monarch colonizers could experience particularly high survival, as the early milkweed shoots would still be relatively free of monarch natural enemies, including ants, aphids, parasitoids, and other invertebrates (Prysby 2004). In fact, this idea was recently verified using citizen science data from the Monarch Larva Monitoring Project (www.mlmp.org), where larval survival was shown to be higher early in the summer compared to late-summer (De Anda and Oberhauser 2015).

In conclusion, based on analyses of 18 yr of citizen science observations, we provide evidence that spring-migrating monarchs are being reported significantly later, by a factor of 1 d later every 4 yr. We also found evidence for a slight (nonsignificant) decline in the range size of the early spring migration, which is primarily composed of adults returning from Mexico. We estimate this decline to be on the order of ∼9% over the last 18 yr. Despite this, we found no evidence that the geographic coverage of the entire recolonization (up to the end of July) has changed over time. We interpret this to mean that while the overwintering population (and early spring migration) appears to be shrinking in size, these early monarchs appear to be compensating with high a reproductive output, which allows the subsequent generations of monarchs to fully recolonize their breeding range in eastern North America.

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