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Tracking the Fall Migration of Eastern Monarchs with Journey North Roost Sightings

New Findings about the Pace of Fall Migration

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We used sightings of fall roosts submitted to Journey North to derive estimates of the pace of migration throughout the central flyway, as well as for discrete time periods within seasons. We regressed the date of all sightings (2005–2011, $n = 1284$) against their latitude to determine the change in latitude per day, which was converted to distance. The migration progresses southward at a rate of 32.2 km/d during fall migration, and the rate is slower in the first half (~13 km/d) than in the second half of the season (~42 km/d). The increased pace is not because the time spent at stopover sites becomes shorter later in the season. Our estimate of migration rate was slower than prior estimates of individual flight speed, because it includes time for both flight and stopover time. The migration rate increased in the 7 years examined, and the first 20 roost sightings from each year increased in latitude over this time. This pattern may be an indication of breeding range expansion, which is occurring now in other nonmigratory butterfly species, and may result in farther migration distances for monarchs. Citizen science data will be critical for identifying future changes in these patterns.

INTRODUCTION

To conserve the migration of monarchs in eastern North America, we need a thorough understanding of all aspects of this migration. In the past decade numerous advances have been made in this area, most notably with the use of citizen science observations. The Journey North program (Journey North 2013) has been especially effective at advancing scientific understanding of both spring and fall migration biology because of its continent-wide scope and wide range of observational data. In this program, participants submit sightings of monarchs online; their observations are used to generate maps that track the spring and fall migrations in real time.

The sightings of nocturnal roosts submitted to Journey North have already been used to track the southward migration flyways of the eastern population; they show one main "central" flyway in North America that points directly to the Mexican overwintering sites, and a second, smaller flyway along the Atlantic coast (Howard and Davis 2009). In addition, a recent study examined the online notes made by observers, including using GIS techniques to document both the actual trees used by roosting monarchs and the landscape characteristics around roost sites. This analysis showed that these "habitat preferences" changed throughout the flyway (Davis et al. 2012a). The primary trees used by roosting monarchs included pines and maples in the northern regions, and oaks, pecans, and willows in the southern United States. Few clear preferences were shown for particular landscape features in selection of roost sites except in the Texas area, where most roosts were in landscapes dominated by grasslands (Davis et al. 2012a).

Here, we use Journey North roost data to estimate the pace of the fall migration. This information will allow us to estimate transit times through regions where habitat conservation is of utmost importance, such as in Texas, where monarchs show a heightened degree of habitat preference (Davis et al. 2012a) and where a lack of nectar resources can have a negative impact on the whole population (Brower et al., this volume, Chapter 10). The ability to estimate changes in the pace of the migration will allow us to assess potential impacts of anthropogenic changes that may alter patterns of fall migration. For example, the removal of agricultural milkweeds from farms in the Midwest (by the use of genetically modified crops that allow for widespread herbicide use, Pleasants and Oberhauser 2012; Pleasants, this volume, Chapter 14), an area that historically produced a large portion of the migratory generation (Wassenaar and Hobson 1998), could alter the fall migration by shifting the breeding distribution away from regions with intensive agriculture. Human activities are also resulting in increasing temperatures, which may cause monarchs to shift their breeding range northward (Batalden et al. 2007). If breeding ranges change over time because of either of these phenomena, we might expect corresponding changes in fall roosting patterns.

Here, we report on the pace of the entire migration, and whether that pace changes throughout the flyway (i.e., does the migration speed up or slow down as the butterflies get closer to their destination?). In addition, we screened the notes associated with a subset of the observations to determine how long monarchs typically spend at roosts and tested whether this changes throughout the flyway. Finally, we put this information into context by summarizing prior estimates of monarch migration rates and flight speed.

METHODS

Journey North roost observations

Detailed descriptions of the Journey North program are provided elsewhere (Howard and Davis 2009, 2011). Briefly, every fall since 2005, Journey North participants have been encouraged to report observations of nocturnal roosts, which monarchs form during their fall migrations, and which can be of any size (often hundreds or even thousands of monarchs). All roost observations are archived online (Journey North 2013). Each observation is associated with a date (of the first night of observation), latitude and longitude (of the center of the town in which the roost was seen), as well as anecdotal notes about the roost itself. For the purposes of this study, we used all fall roost data from 2005 through 2011. Furthermore, we used roosts only in the primary, central flyway, as defined in a prior study (Howard and Davis 2009), since monarchs from Atlantic coastal locations make up only a small fraction of the overwintering cohort in Mexico (Wassenaar and Hobson 1998); thus, we did not include data from states or provinces on the Atlantic coast. These criteria resulted in a total of 1284 roost observations over seven years (Figure 18.1), although some locations were represented in multiple years, and even multiple times within years if two roosts were seen in the same town. The sample sizes for each year, from 2005 through 2011, were 178, 143, 231, 129, 153, 296, and 154, respectively.

Estimating migration pace

Since monarchs are moving primarily southward during the fall migration, the latitude of roost sightings becomes progressively lower over the course of the migration season (Howard and Davis 2009). With this in mind, we plotted the latitude of all sightings in a given year against the date of the sighting (in days since 1 January), resulting in a scatterplot with a downward-pointing pattern for each year (Figure 18.2). Then, we fitted a linear regression line to these data, with the slope of this line representing the *rate of reduction in latitude per day*, or in other words, the pace of the *southward* migration. Using this regression approach we obtained a single value for each year that reflects the average southward pace of the entire migration throughout the whole flyway, although this number does not take into account possible variation within seasons, which was one of our goals. Therefore, we obtained separate rates (using the procedure above) for four time periods within each season, which we arbitrarily defined as 20-day intervals starting at day 220 (10 August) and ending on day 300 (27 October). The number of roost sightings within each time interval (1–4) was 185, 412, 368 and 287. While the migration continues past 27 October, insufficient data points were reported beyond 27 October to analyze. In the end we had estimates of migration rate (i.e., slopes of the time-latitude plots) for 4 time intervals over 7 years ($n = 28$) for statistical analyses (see below).

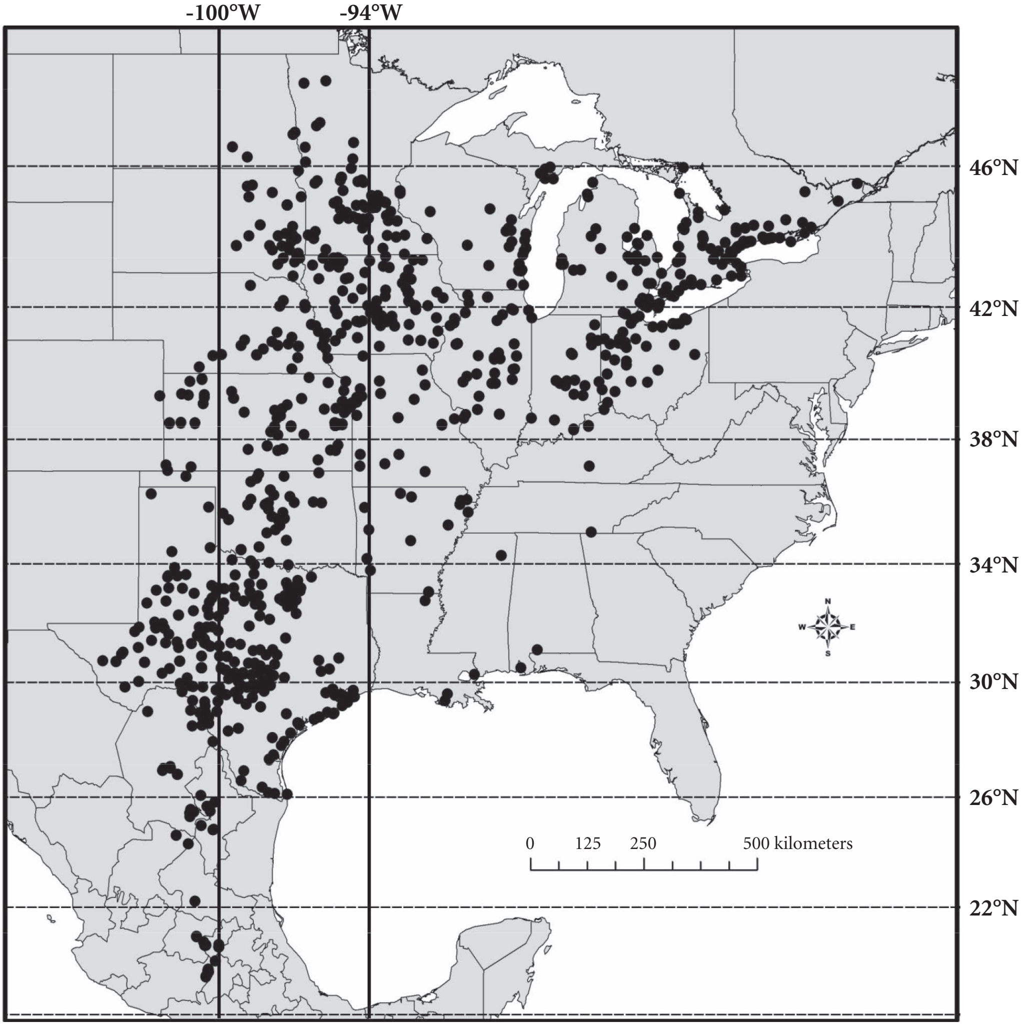

Figure 18.1. Locations of monarch roost observations submitted to Journey North between 2005 and 2011. Note that roosts from states bordering the Atlantic Ocean are not shown; this study used roost observations from only the main "central" flyway. Solid vertical lines indicate region used to examine the pace of "southward-only" migration (see methods for description).

Early in the migration, the primary flight direction for monarchs from the northeastern United States is to the southwest (Figure 18.1). This direction may result in slower rates of southward advancement in the early phase of the fall migration; therefore, we repeated the steps above (linear regression of date and latitude) for a narrow range of roost sightings running down the approximate center of the flyway (from −100°W to −94°W longitude, see Figure 18.1). Restricting the analysis to these points ensured that the estimates of migration pace reflected "southward-only" advancement. Too few roosts were sighted in certain years to obtain separate rate values for each time period, so for this subset we determined the annual migration rate for periods 1 and 2 combined, and for periods 3 and 4 combined.

Roost duration

For a subset of the roost data (2005–2008) we screened the written notes submitted along with the observations, recorded how many nights the roost was occupied, and categorized these data according

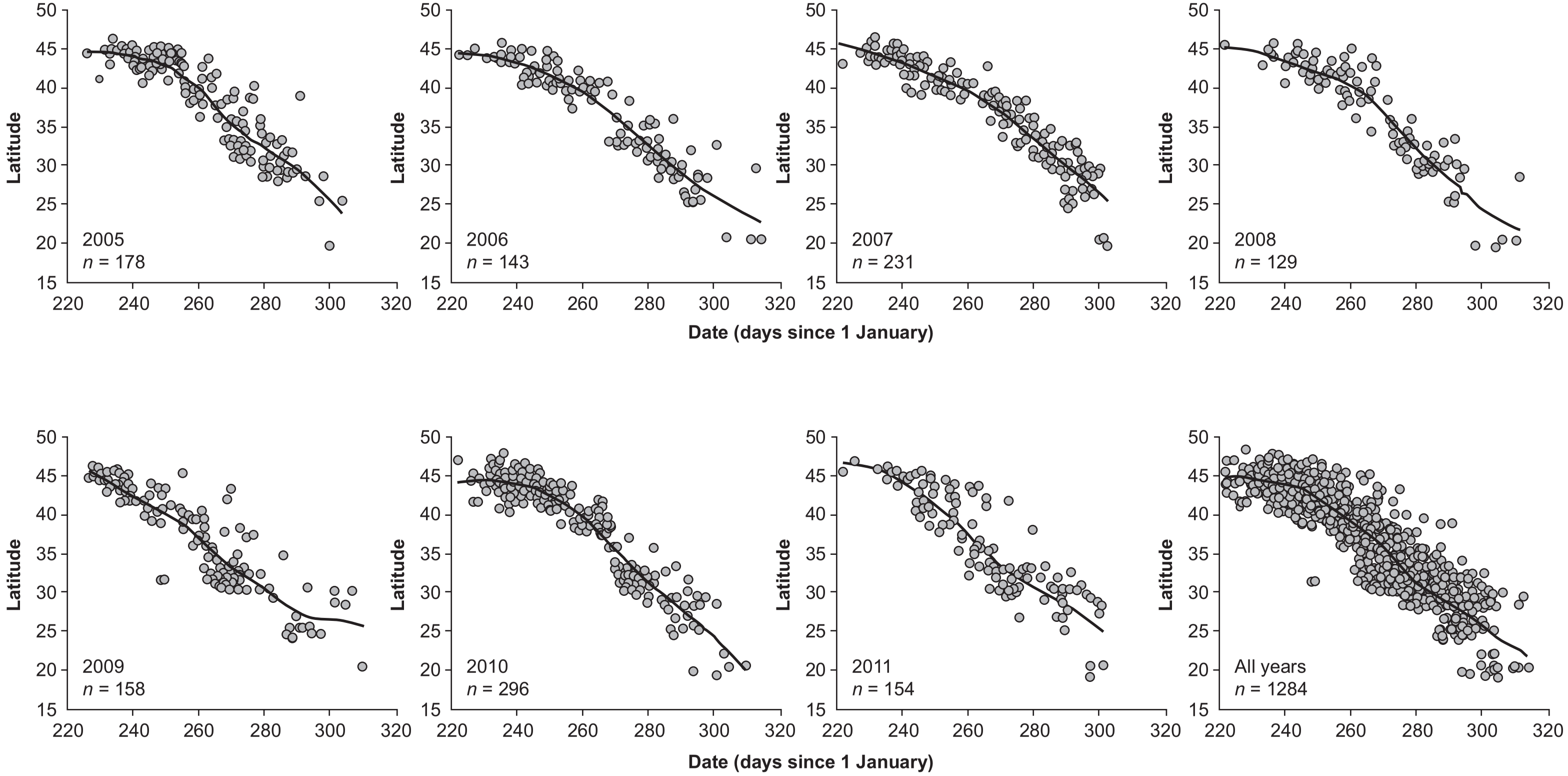

Figure 18.2. Plots of the latitudes of roost observations (*y*-axes) in relation to the date (in days since 1 January, *x*-axes) for all years separately and combined. A distance-weighted least-squares regression line is fitted to each plot.

to the four 20-day time intervals indicated above. Since not all observations contained this information, the final sample size here was $n = 158$.

Data analyses

We examined the migration rate data from the entire flyway (the slopes of the time-latitude scatterplots, $n = 28$) with a two-way ANOVA, where the time interval and year were predictor variables. Year was included as a categorical predictor variable, since we had no a priori expectation of an increase or decrease over the years of the study (but see results). This test therefore examined whether the rate of migration changed over time within each season, and whether it was different from year to year. We next examined the rates obtained using the subset of roosts from the center of the flyway (see Figure 18.1). Here, we compared the rates of the first half of the migration (periods 1 and 2, pooled, $n = 7$) to those from the second half (pooled, $n = 7$) using a t-test. The data set reflecting the roost durations ($n = 158$) was not normally distributed, so we log-transformed (+1) these values to approximate a normal distribution. We used a two-way ANOVA to examine roost durations across the 4 time intervals with year included as a categorical variable, although we had data spanning only 4 years in this subset.

RESULTS

With roost observations from all years considered together, including those after 27 October, the slope of a linear regression line fitted to the time-latitude graph (Figure 18.2) was −0.29. In other words, the migration progressed southward at a rate of 0.29° (or 32.2 km) per day. In the ANOVA examining migration rates within seasons, there was no effect of year ($F_{6,18} = 1.54$, $P = 0.221$) when it was included as a categorical predictor (but see below); however, the pace of the migration did vary with time interval ($F_{3,18} = 26.07$, $P < 0.001$). To depict this variation, the average rates across intervals are graphed in Figure 18.3. Based on Tukey's post-hoc tests, the rates for the first two time intervals (10 August–17 September) were not significantly different from each other, nor were the rates of the last two intervals (18 September–27 October); however, the pace of the migration (i.e., the rate of southward-only movement) approximately doubled in the second half of the fall season; in the first half it was between −0.06° and −0.17° latitude (7–19 km/d, or a combined average of 13 km/d), and in the second it is between −0.32° and −0.42° per day (36–47 km/d, or a combined average of 42 km/d). The relatively slower pace of the initial part of the migration can also be visualized by closely examining Figure 18.2. In most years there is little to no southward movement near the beginning of the season; this is especially evident if a distance-weighted regression line is fitted to the points. Examination of migration rate for the subset of roosts between −100°W and −94°W longitude showed a similar pattern; a significantly slower average pace during periods 1 and 2 (mean = −0.22°/d) compared with periods 3 and 4 (mean = −0.31°/d; t-test, df = 12, $t = 3.45$, $P = 0.005$). The faster early migration for this subset (0.22°/d vs. 0.06°–0.17°/d) reflects the fact that butterflies moving southwest were removed from the analysis.

On average, roost durations lasted about 2 nights considering all roost observations for which we had this information ($n = 158$). There was no significant change in durations across time intervals ($F_{3,151} = 2.07$, $P = 0.107$). We found an unexpected effect of year ($F_{3,151} = 3.53$, $P = 0.016$), but upon further examination it appears this effect was driven by one year,

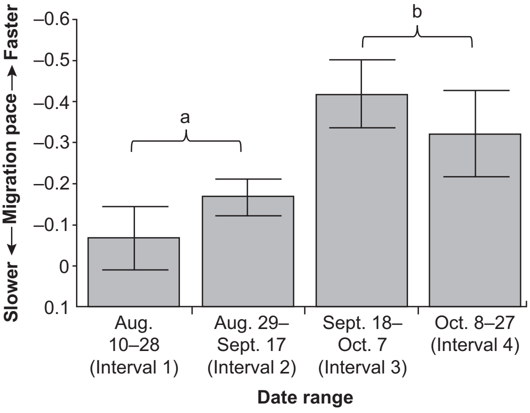

Figure 18.3. Average migration rates during the four date ranges (time intervals) used in this study. Rate was the slope of the regression line in a plot of latitude versus date, so values indicate the degrees of latitude covered per day (they are negative because latitudes become lower as the migration progresses southward). Values on the y-axis are shown in reverse order so that faster rates are at the top. Whiskers on bars represent 95% confidence intervals. Letters above bars indicate homogeneous groups based on Tukey's post-hoc tests.

2008, when roost durations averaged about 3 nights in length (significantly greater than other years, Tukey's post-hoc tests, $P = 0.020$).

Finally, when we inspected the migration rates for each year, we noticed that the annual rates appeared to be increasing over subsequent years. To test this observation, we examined the same data using ANCOVA, with time interval as a predictor as before, but with year included as a continuous covariate. This approach takes into account the ordinal nature of year (i.e., 2007 follows 2006, which follows 2005, etc.), which the ANOVA does not. Again there was an effect of time interval ($F_{3,23} = 29.29$, $P < 0.001$), but more importantly, in this model the effect of year was significant ($F_{1,23} = 7.62$, $P = 0.011$). The direction of this effect can be seen in Figure 18.4; when we averaged the 4 slope estimates (from each time interval) for each year and plotted them against year, there was a highly significant correlation ($r = -0.86$, $P = 0.014$). In other words, within the 7 years of data examined here, it seems that the migration progressed faster over time. To ensure that this pattern was not an artifact of increasing participation in Journey North observations, we compared the number of roost observations with year using Pearson correlation and found no significant relationship ($r = 0.20$, $P = 0.664$). To help interpret this pattern we extracted from the roost data the first 20 sightings from each year and compared their latitudes and dates across years. There was a small but positive correlation between year and latitude ($r = 0.21$, $p = 0.013$), but no relationship between date and year ($r = 0.02$, $P = 0.734$). This means that the fall migration did not change in terms of when it started, but in the 7 years we examined the first roosts sighted shifted northward (from about 44°N latitude to about 45°N, or about 100 km).

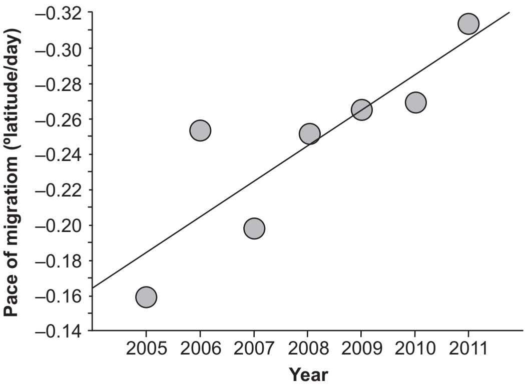

Figure 18.4. Plot of the annual pace of fall migration from 2005 to 2011. Each point on the graph represents the average rate (slope of the time-latitude graph, in degrees per day) of the 4 time intervals. $R = -0.86$, $P = 0.0139$. Values on the vertical axis are reversed so that faster rates are higher.

DISCUSSION

Journey North roost data indicate that the overall southward pace of the fall monarch migration is about 32 km/day. In other words, new roosts are formed about 32 km farther south than in the prior day (although this does not take into account variation within seasons; see below). This pace is not an estimate of the flight speed of individual butterflies; rather, this estimate includes both flight and stopover time (the latter reflecting time for feeding, resting, and waiting for appropriate wind and weather conditions). To demonstrate this point, we compiled a list of published and unpublished estimates of individual flight speed of monarch butterflies (Table 18.1). Assuming that migrating monarchs spend approximately 10 hours per day in flight, our daily estimate translates to about 3.2 km/hour, on the low end of flight speed estimates (Table 18.1). For example, Moskowitz et al. (2001) watched individual monarchs flying during one fall day (when exceptionally large numbers were flying) and estimated their flight speed at 7.2 km/h. Garland and Davis (2002) reported that a tagged monarch flew 226 km in a single day (although with a strong tailwind), a speed of approximately 14 km/h. On the other hand, in terms of the pace of the entire migratory cohort, the estimate we obtained here is consistent with dividing the total distance of the migration by the total time of the migration. If we consider the entire migration distance of approximately 3000 km (from northern Minnesota to Central Mexico), and the typical duration of the entire migration season, which is roughly 85 days (based on first roost reports and the arrival dates at the overwintering sites), the result is 35 km/d.

As we found with the spring migration (Davis and Howard 2005), the pace of the fall migration varies throughout the season; the migration appears to speed up in the second half of the season. The seemingly slow pace of the migration in the first half may be partly influenced by the fact that many of these

Table 18.1. Summary of published and unpublished estimates of monarch flight speed

Season	Estimate	Method of estimation	Source
Fall	18 km/h	Tracking "cruising" monarchs by car (and reading car speedometer).	Urquhart 1960
Fall	14 km/h	Calculated from the recapture of a monarch in eastern Virginia that was tagged the previous day at Cape May, NJ (226 km away). There was a strong tailwind that day.	Garland and Davis 2002
Fall	7.5 km/h	Derived from the time it takes the fall migration wave front to go from Minnesota to the Mexico border (~2250 km over 30 days, or 75 km/d).	MonarchWatch website
Fall	7.2 km/h	Viewing low-flying migrating monarchs as they passed by an open parking lot during an exceptionally large flight day in fall 1999.	Moskowitz et al. 2001
Fall	3.9 km/h	Average speed of 100+ healthy monarchs when attached to a flight mill and monitored remotely by computer. All were reared in captivity under late summer conditions.	Davis et al. 2012b
Spring	71.5 km/d or 7.2 km/h	Using GIS to measure rate of expansion of the spring migration wave front from sightings of adults submitted to Journey North. Average rate over 7 years used here.	Davis and Howard 2005
Spring	24 km/d or 2.4 km/h	Based on the slope of a regression of oviposition date and latitude.	Cockrell et al. 1993

Notes: Data in this table are for comparison with the estimate of migration pace from this study (which takes into account both flight time and stopover time). In cases where rates or speeds were reported in km/d, we report them here as km/h, assuming monarchs fly for 10 hours in a day.

monarchs are migrating southwest (Figure 18.1), reducing the overall rate of southward advancement; however, restricting our analyses to the subset of roosts observed in the center of the flyway (so that only southward movement is captured, Figure 18.1) also showed slower average rates in the first half of the migration. We also point out that the total number of roost sightings in the first half of the migration (*n* = 597) was roughly equivalent to the total number in the second half (*n* = 655), meaning these results should not have been influenced by uneven distribution of observers. Thus, we can be confident in concluding that the rate of southward advancement really is slower during the first half of the migration.

Given the difference in migration pace throughout the flyway, it seems surprising that roost *durations* did not vary over the course of the season; roosts tended to last about 2 nights on average, regardless how far along the migration was. If the overall migration pace quickens as the cohort moves south, one would expect roost durations to shorten as the migration advances (if monarchs spend less time at stopover sites). A possible explanation for this apparent discrepancy lies in our assumption that roost "durations" reflect actual stopover lengths of individual monarchs, which may or may not be the case, and can really be addressed only by using tagging data. In fact, two prior investigations using tagging data found that individual stopover lengths were actually longer in the southern site (in South Carolina) than in a more northern site (in Virginia) (Davis and Garland 2004; McCord and Davis 2012). Thus, if the migration advances more quickly as the season progresses, it does not appear to be because the time spent at stopover sites becomes shorter. If this is the case, then the only other explanation is that the monarchs must cover more ground during the day as the season progresses, either with faster individual flight speeds or by simply flying with fewer temporary daytime stops at ground sites.

Perhaps the most intriguing result of this study was the one we did not set out to examine; over the 7 years of roost observations we examined (2005–2011), the pace of the fall migration increased (Figure 18.4). This trend should be monitored closely in the future; indeed, there are good reasons to expect that certain aspects of the fall migration will change because of climate change (Batalden et al. 2007) or the loss of agricultural milkweeds (Pleasants and Oberhauser 2012), either of which could shift breeding ranges. In fact, this may already be happening. The northward shift in latitudes of the first roost sites each year suggests that the breeding areas of monarchs may be shifting northward, a phenomenon that was predicted to occur in response to climate change (Batalden et al. 2007). Climate-driven, northward range expansions are also being seen in other (nonmigratory) butterfly species (e.g., Crozier 2004b; Finkbeiner et al. 2011; Pateman et al. 2012). If this trend continues with eastern monarchs, their overall migration distance will also increase (assuming the ultimate destination will remain the overwintering sites in Central Mexico). Given the many risks associated with long-distance migration (McKenna et al. 2001; Howard and Davis 2012), anything that prolongs this sensitive period could ultimately result in fewer monarchs surviving the migration.

Finally, we point out that the information obtained in this study highlights how advances in monarch conservation and biology can be, and are continuing to be, made possible thanks to the dedication of the citizen scientists who participate in this and other monarch monitoring programs. Only by using large-scale data sets covering many years can we address important questions relating to migration pace, habitat selection, and climate impacts. With the answers to each new question, our ability to conserve this fascinating insect continues to improve.

ACKNOWLEDGMENTS

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