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SPRING RECOLONIZATION RATE OF MONARCH BUTTERFLIES IN EASTERN NORTH AMERICA: NEW ESTIMATES FROM CITIZEN-SCIENCE DATA

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ABSTRACT: Monarch butterflies in eastern North America return each year from their overwintering site in central Mexico to recolonize their range in the eastern US and Canada. Current knowledge of the spring recolonization rate (i.e the rate of advancement) comes from observations of eggs and larvae along a latitudinal gradient. Journey North is a website-based program whereby citizen-scientists report their first sightings of adult monarch butterflies each spring. We used 7 years of this sighting data combined with GIS technology to derive new estimates of the rate of monarch recolonization based on the cumulative area occupied and the rate of movement of the advancing wave front. We further used these data to examine differences between and within years (we divided each season into 12 time intervals) in the recolonization rate. Across all years, the average rate of recolonization was 71.6 km/d. We found no statistical difference between the annual (season average) estimates, which ranged from 66.6 to 78.1 km/d. Within seasons, we observed 4 distinct phases of the spring migration, consistent with previous work, and there was significant variation within years (i.e. between time intervals) in the rate of recolonization, with the migration wave front progressing the fastest (over 100 km/d) from 20 March to 9 April, and from 19 May to 29 May. Based on these new estimates, we conclude that the spring migration of monarch butterflies in eastern North America progresses faster than previously estimated, and the temporal patterns observed each year are remarkably constant.

Each spring, monarch butterflies (*Danaus plexippus*) in eastern North America return from their overwintering site in central Mexico to repopulate their breeding range, ultimately reaching most US states and Canadian provinces east of the Rocky Mountains. This fascinating journey is made even more complex by the fact that recolonization is completed by two successive generations of monarchs (Cockrell et al. 1993, Malcolm et al. 1993, Brower 1995). Many monarchs at the overwintering colonies mate before migrating north in the spring (Van Hook 1993, Oberhauser and Frey 1997). As they migrate northward, the mated females then lay eggs on the newly emerging milkweed plants. Although the exact distance traveled by these first-generation females is difficult to ascertain, evidence suggests that this recolonization process is accomplished in two or three phases. Adults returning from Mexico travel as far north as 35° latitude, or the southern portion of the United States (Cockrell et al. 1993) before they die. The offspring and grand-offspring derived from these eggs then complete the second and third phase of the journey northward to the northernmost areas of the monarchs' breeding range in the northern US and southern Canada. This recolonization process has been referred to as the 'successive brood' migration strategy (Malcolm et al. 1993).

Much of what is known about the timing of monarch recolonization is the result of a comprehensive study published by Barbara Cockrell, Stephen Malcolm and Lincoln Brower (Cockrell et al. 1993). In this study, detailed observations of spring oviposition timing were recorded over three successive years at many locations throughout the monarchs' eastern range. The authors provided evidence for the successive brood migration strategy, and demonstrated that the rate of recolonization northward does not proceed at a constant speed, but varies due to the lag of larval development of the second brood midway through the migration.

A decade later, our knowledge of the monarchs' spring migration has improved, largely due to the internet-based, citizen-science program called Journey North (http://www.learner.org/jnorth/). Established in 1994, Journey North is a web-based citizen science program where school children, educational groups and other volunteers throughout North America report the first sighting they make of an adult monarch butterfly each spring. The date and location of the sighting are recorded by the participants online and these data are archived by Journey North staff. At regular intervals during the spring, the sightings are plotted on a map of North America by Journey North staff, allowing the online participants to view their sighting along with other sightings from around North America. When all observations are combined and plotted by Journey North staff, viewers can see the northward progression of the monarchs' spring migration via the timing of participant sightings.

Although the Journey North program is used primarily as an educational tool for teachers, the data generated by the program have demonstrated their scientific value in increasing our knowledge of this critical phase of the monarch life cycle. We used the first 6 years of the Journey North data in a previous paper to document the state-by-state pattern of spring migration in the eastern North American population (Howard and Davis 2004). By using the timings and locations of monarch 'first sightings' reported by Journey North participants throughout the spring migration range we showed that there was an annual and nontrivial eastward movement of monarchs from southern Texas along the southeastern states before the migration wave front proceeds northward.

In the present paper, we used 7 years of Journey North data combined with GIS technology to derive updated estimates of the rate of spring recolonization based on both northward and eastward movement from southern Texas (which we used as the 'starting point' for the migration). We also used these revised rate data to determine if the rate of recolonization varies between and within years.

METHODS

Calculating recolonization rate. Journey North data consisted of citizen-science observations of first sightings of monarchs every year (usually between March and July for the spring migration), which includes the year, date and location (latitude, longitude) of the sightings. Further details of the Journey North data collection protocols have been addressed previously (Howard and Davis 2004) and are online at http://www.learner.org/jnorth/. We used data from 1997 to 2003 for this study. To measure the recolonization rate we used a method similar to that used by researchers to track the spatial spread of species invasions (reviewed in Shigesada and Kawasaki 1997) and infectious diseases (e.g. Dhondt et al. 1998). We calculated the area occupied by monarchs at successive time intervals during the spring to estimate the rate of expansion of the outer edge of the recolonized area. To derive time intervals we divided the Journey North data for each spring into 12 intervals of 10 days each. These intervals began and ended on the same julian dates each year (March 1 to July 28). We then digitally plotted the point locations of each Journey North monarch observation (based on the associated spatial coordinates of each sighting) onto a map of eastern North America using ArcView version 3.2a (Environmental Systems Research Institute, Inc., Redlands, CA, USA). For each 10-day interval in each year, we manually traced the smallest possible polygon around the outermost monarch observations that were made within that time interval (Fig. 1). Thus, each year as the migration expanded in each successive time interval, so did the size of the cumulative area within each successive polygon. We calculated the area of each polygon (in square kilometers) with a simple ArcView function. All polygons were drawn over land area only, and did not extend over ocean areas. Furthermore, to ensure that we were tracking the spread of monarchs that originated only in Mexico, we conservatively drew polygons over monarch sightings that took place only at 30 degrees north latitude and above.

To estimate the recolonization rate for each 10-day time interval we determined the amount of increase in polygon area from one 10-day interval to the next (km^2/d), then calculated the square root of this value to obtain an estimate of the linear rate of increase (km/d) over the 10-day interval. Dividing this value by 10 resulted in the rate (km/d) of recolonization per day. This value then represented our estimate of the speed (per day) at which the leading edge of the migration wave front progressed outward (which we infer to represent monarch recolonization) in all directions for each of our time intervals. Since we calculated the area of 12 time intervals, and our rate estimate is based on the difference in area between successive intervals, we ended up with 11 estimates of recolonization rate per season (or migration), over 7 seasons.

Statistical Analysis. To test for differences in the recolonization rate between intervals and years, we performed a univariate ANOVA using our recolonization rate estimates as the dependent variable, and using year as a fixed factor and time interval as a cofactor. An interaction effect between year and time interval was also included. This analysis was performed using SPSS software (SPSS 2001), and significance was accepted when $p<0.05$.

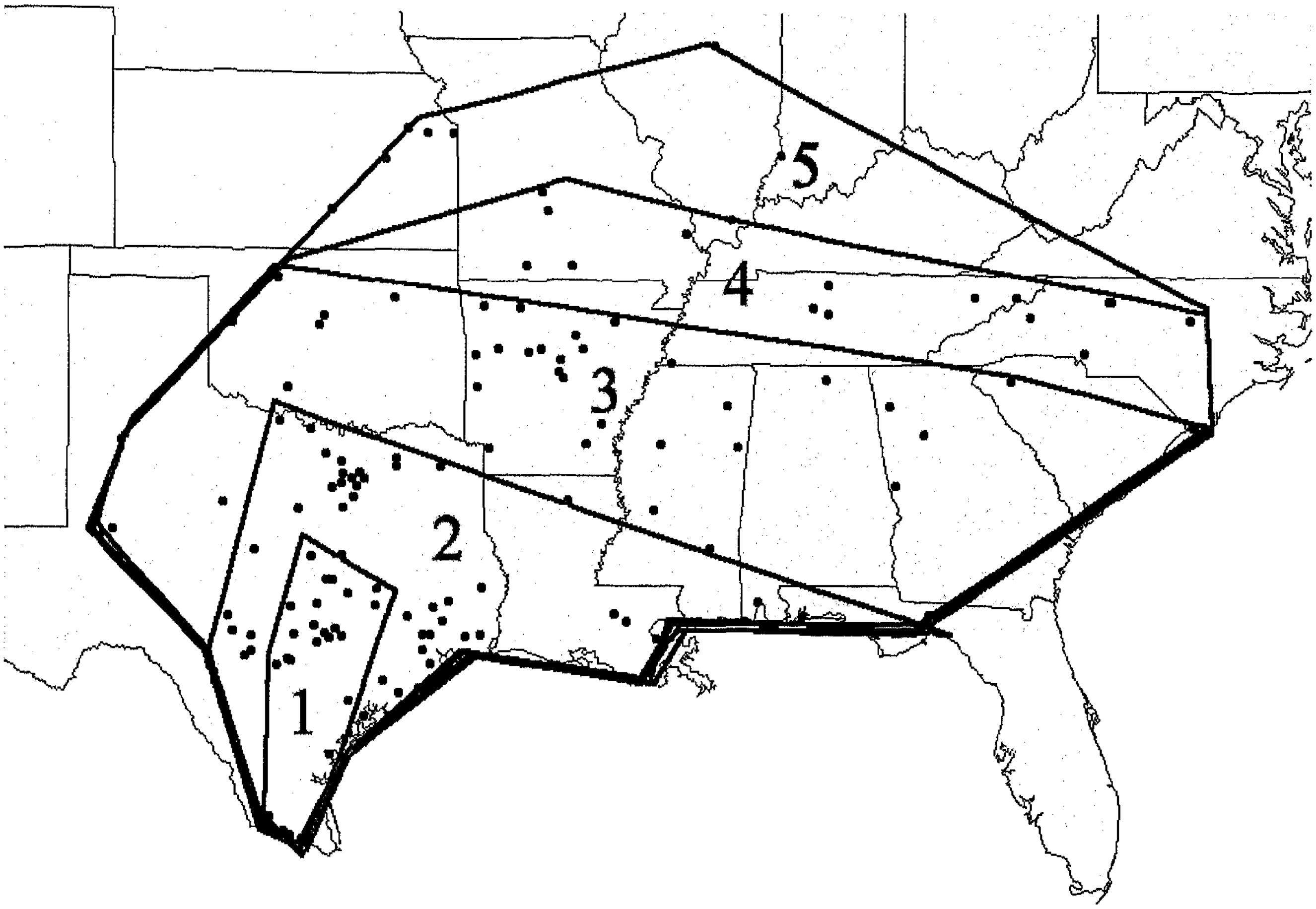

FIG. 1. Method used for assessing the recolonization rate of monarch spring migration using Journey North sightings. All monarch sighting locations (black dots) were plotted in Arcview (version 3.2). For each 10-day interval the smallest possible polygon was drawn around the sightings (dots) in that interval. The increase in area between successive polygons was calculated and the migration speed was calculated as the square root of this area increase. Numbers in figure denote successive 10-day time intervals.

RESULTS AND DISCUSSION

The average rate of recolonization across all years and all time intervals was 71.6 km/d, with the annual average ranging from 66.6 to 78.1 km/d over the 7 years examined in this study (Table 1). Maximum rates each year ranged from 111.0 to 165.9 km/d, and there was significant variation in the recolonization rate between intervals (df=1, F=20.1, p<0.001; Fig. 2). The 7-year average rates shown in figure 2 indicate that monarchs usually recolonized their range the fastest during the 3rd, 4th and 9th time intervals. We detected no significant effect of year on the recolonization rate with our analysis-of-variance test (df=6, F=0.101, p=0.996), nor was there a significant interaction between interval and year (df=6, F=0.155, p=0.987). The lack of a significant interaction effect between year and time interval in our ANOVA test indicates that there was little annual variation in this overall pattern (i.e. with respect to the rate) of spring recolonization. This result is not surprising, given the similar results we previously described, that there is little annual variation in the spatial pattern (i.e. state by state occupation) of migration (Howard and Davis 2004). Combined, these results speak to the consistent nature of the spring migration.

The estimates of recolonization rate we derived differ considerably from previous estimates. Before it was known that the spring migration is composed of two sets of cohorts, an early estimate of the spring recolonization rate was 4 km/day, assuming a constant rate of travel throughout the spring (Baker 1978). Cockrell et al. (1993) revised this estimate based on their observations of spring oviposition timing. They estimated a northward (only) rate of recolonization of 14 km/d, assuming a constant rate of travel. They also demonstrated how the spring migration can be divided into 4 time phases and calculated rates of 96.0, 12.4, 52.0, and 8.2 km/d for each phase, respectively (Fig. 3). Our maximum rate over all intervals in all 7 years was 165.9 km/d, considerably greater than the maximum

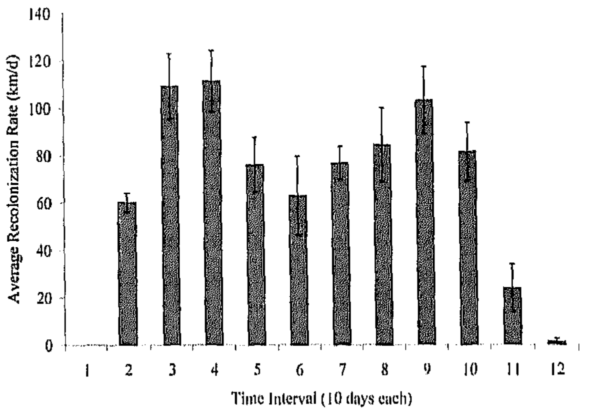

FIG. 2. Mean recolonization rate from one 10-day interval to the next over the 7 years studied. Standard error bars shown. Intervals begin on 1 March and end on 28 June.

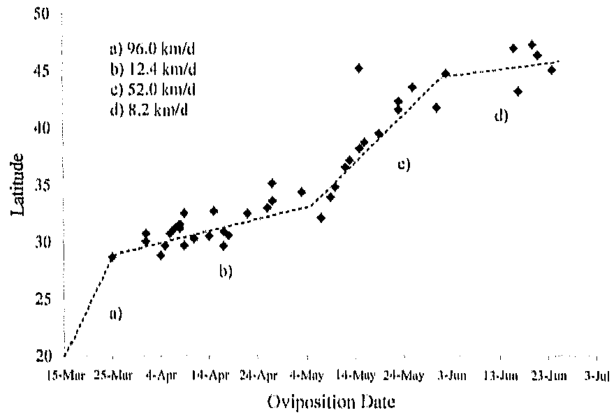

FIG. 3. Plot of timing of spring oviposition in relation to latitude, as shown in Cockrell et al. (1993). Reproduced with permission.

TABLE 1: Monarch spring recolonization rate estimates (in km/d) calculated for each 10-day interval in each year examined in this study. Rate calculated by determining the increase in geographic area occupied by the migration wave front from one time interval to the next (expressed in km2), deriving the square root of the increase (expressed in km), and dividing by 10.

Int[a]	Date[b]	1997	1998	1999	2000	2001	2002	2003	Average
2	10-Mar	61.3	75.9	52.4	53.1	61.2	46.3	70.9	60.2
3	20-Mar	157.8	69.7	98.8	102.2	63.5	150.9	119.7	108.9
4	30-Mar	110.1	128.0	165.9	133.1	94.6	71.0	74.5	111.0
5	9-Apr	46.8	105.9	53.0	81.9	127.8	55.4	59.5	75.8
6	19-Apr	0.0	29.9	29.7	82.9	126.6	77.3	92.2	62.7
7	29-Apr	94.6	58.3	86.4	93.4	54.4	58.0	88.9	76.3
8	9-May	62.2	153.7	66.5	43.5	126.5	53.0	83.0	84.1
9	19-May	77.6	38.5	108.2	107.6	96.4	147.7	141.2	102.4
10	29-May	129.1	26.2	101.5	94.0	66.3	72.5	76.8	80.9
11	8-Jun	49.6	61.2	0.0	11.8	0.0	0.0	43.3	23.7
12	18-Jun	0.0	0.0	0.0	0.0	0.0	0.0	8.7	1.2
Average		71.7	67.9	69.3	73.0	74.3	66.6	78.1	

[a] Interval - recolonization rates shown in each time interval are based on increases in migration wave front area between it and the previous time interval. Interval 1 not shown.
[b] date of the first day of each 10-day interval is show

rate obtained by Cockrell et al. (1993), of 96 km/d. However, despite being collected over a decade apart, and with two completely different methods, the data gathered by citizen-scientists in the Journey North program and that of Cockrell et al. (1993) show some remarkable similarities. For comparison with the results from that study, we plotted the area encompassed by the migration front at each time interval (Fig. 4). In this plot, one can distinguish the same 4 phases described by Cockrell et al. (1993; Fig. 3) in most years. For the most part, the spring recolonization (from Texas) begins with a rapid increase in area in intervals 2,3 and 4, which corresponds roughly to the first three weeks of April. The expansion then slows until interval 8, when it undergoes another rapid increase in area. The entire migration always slows and reaches a plateau by interval 11 (which begins on June 8). Interestingly, Fig. 4 also indicates that by the end of the migration each year, there is little variation in the size of the geographic range occupied by monarchs.

Since the Cockrell data is based on latitudinal movement, another useful comparison of these two data sets would be to create estimates based on latitudinal movement from the Journey North data. We did this by plotting the latitude of all 7 years of Journey North observations up to July 27 (2912 records) against its date (Fig. 5), which was done in the Cockrell paper. When a linear regression line is fitted to this data, the slope of the line indicates the overall rate of northward (latitudinal) recolonization, assuming a constant rate of

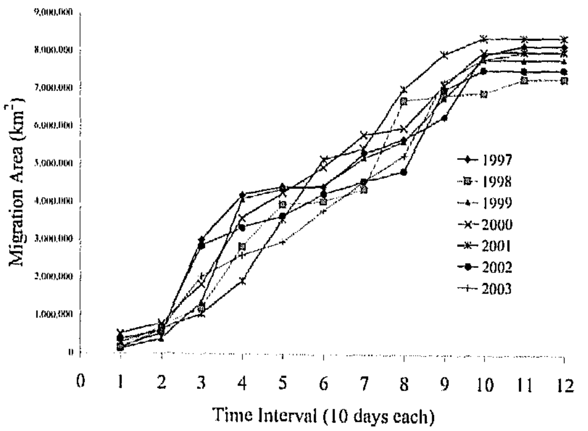

FIG. 4. Plot of the increase in area (km²) occupied by the monarch migration in each 10-day interval for each year. Intervals begin on 1 March and end on 28 June.

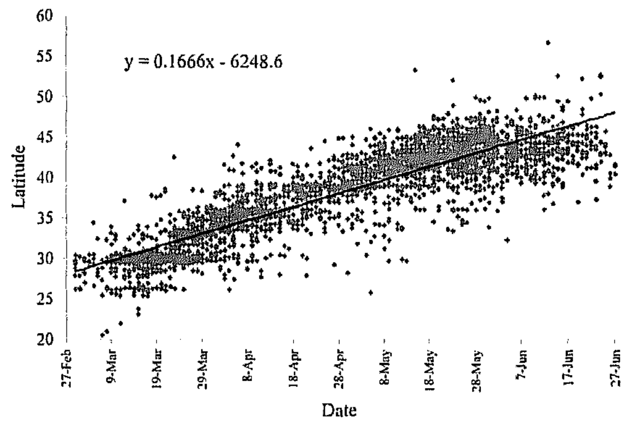

FIG. 5. Relationship between latitude and date using all Journey North spring monarch sightings from 1997-2003 up to July 27 (N=2912). The slope of the trendline (0.1666° lat./day) indicates a northward (only) recolonization rate of 18.4 km/day

progression throughout the migration. For the Journey North data, the slope of this line was 0.16 degrees of latitude per day, which translates to 18.4 km/d (1 degree latitude equals 110.6 km). The slope of the same regression line in Cockrell et al. (1993) indicated a rate of 14 km/d.

We conclude that the rate of advancement of the spring recolonization proceeds faster than previously described, although the overall pattern of recolonization is remarkably consistent year to year. Further, based on the similarities with previous results obtained, we conclude that the citizen-science based data gathered by Journey North is a valid scientific resource and is as accurate in tracking migration patterns as scientific observers.

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