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Connecting Eastern Monarch Population Dynamics across Their Migratory Cycle

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The eastern North American monarch population has a complex annual cycle with four phases: (1) aggregation of most individuals within a small overwintering zone in Mexico; (2) northward spring migration and breeding through the southern United States; (3) summer expansion and breeding throughout the eastern United States and southeastern Canada; and (4) autumn migration to the same overwintering sites. We followed monarch population dynamics throughout this annual cycle, using data from seven large-scale monitoring programs, most relying on citizen scientists. We looked for evidence that dynamics at one step of the migratory cycle carry over to subsequent steps using linear regression. Our results confirm earlier findings that dynamics during the spring recruitment phase have a critical influence on the ultimate size of the breeding population each year. We also found a disconnect between summer and winter numbers that deserves further study. We highlight the need to reexamine these results as new data continue to become available, to develop models that can tease apart multiple interacting factors, and to bolster monitoring programs where data are currently lacking, especially during the spring migration.

INTRODUCTION

The eastern migratory population of North American monarchs (hereafter, “monarchs” refers to the eastern population unless otherwise specified) follows a fairly consistent annual pattern (Figure 24.1). Individuals that have spent the winter at overwintering sites in central Mexico fly north to lay eggs in northern Mexico and the southern United States. Those offspring then travel to the summer breeding grounds in the north-central and northeastern United States and southern Canada that produced their parents’ generation the year before. There they breed and produce two to three additional generations. In late summer and early fall, the last generation undergoes a southward migration and travels to the overwintering colony sites, where it remains until the following spring, when the cycle repeats. Thus, the population can be characterized by fairly consistent spatial and numerical expansion each

year, followed by contraction into wintering sites, a period during which little reproduction occurs. We refer to this pattern of migrating north, expansion and breeding, migrating south, and overwintering as the monarch annual life cycle (or annual cycle) to distinguish it from the individual life cycle of egg, larva, pupa, and adult.

There are deviations from this “normal” annual cycle. During the winter some monarchs remain in southern regions of the United States and reproduce (Prysbly and Oberhauser 2004; Howard et al. 2010; Batalden and Oberhauser, this volume, Chapter 19) and some winter breeding occurs in Mexico (Oberhauser, pers. observ.). Even the existence of an eastern population completely distinct from the West is probably a myth (Pyle, this volume, Chapter 21); however, the evidence is overwhelming that the cycle described above characterizes the vast majority of a monarch population that is largely spatially separated from the population in the West. Even

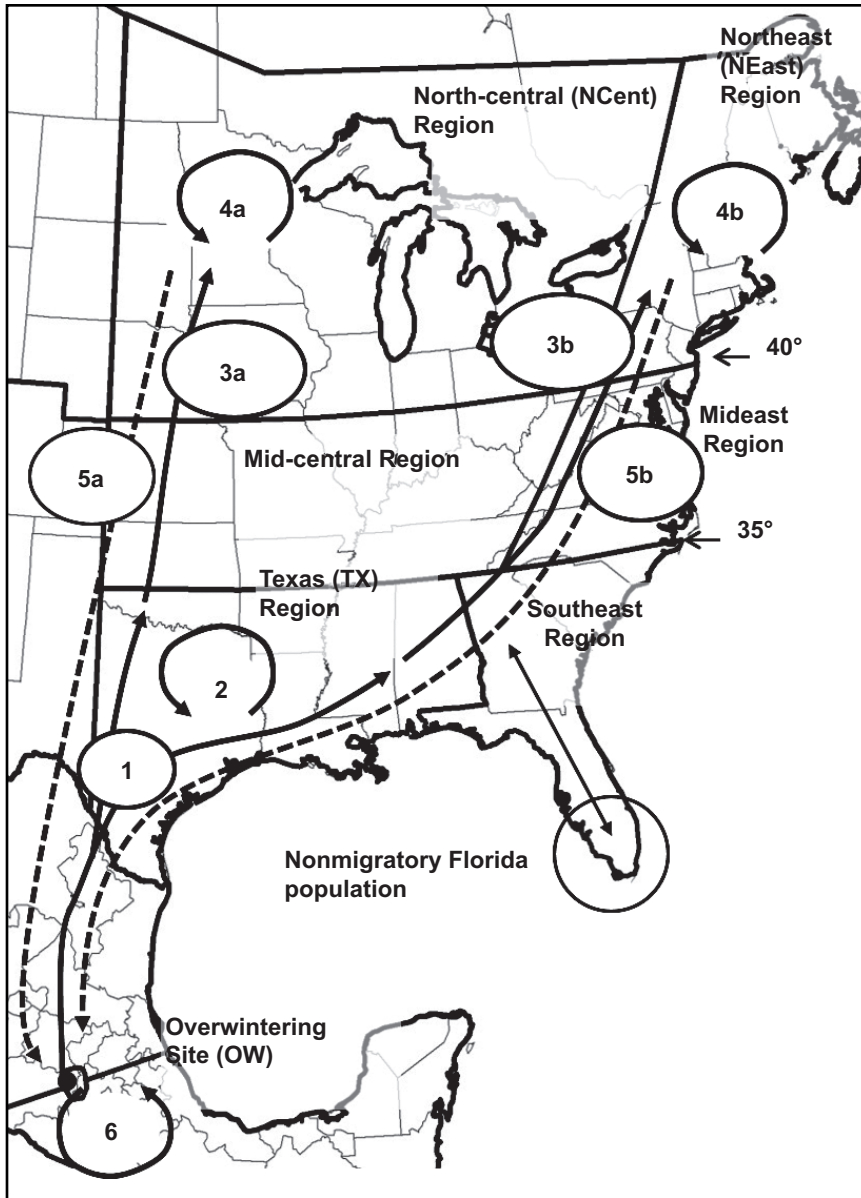


Figure 24.1. Range map of the eastern migratory population of monarchs illustrating major steps in their annual cycle. Arrows and numbers represent transitions from one stage of the cycle to the next, which often involve movement from one region to another. Steps include: (1) Spring migration from overwintering sites in Mexico. (2) Reproduction by the migratory generation to produce first new generation of the year in the southern United States (Texas region). (3) Migration to the North-central (3a) and Northeast (3b) regions. (4) Reproduction and population build-up in the North-central (4a) and Northeast (4b) regions. (5) Fall migration from the North-central (5a) and Northeast (5b) regions. (6) Overwintering in Mexico from late fall through early the following spring.

though this population is widely distributed during the summer, it nonetheless constitutes a single, cohesive population, as documented by Eanes and Koehn (1978) and several subsequent studies (summarized by Pierce et al., this volume, Chapter 23). Thus, data collected throughout eastern North America can

inform our understanding of what is happening to the population as a whole.

Recent evidence suggests that the eastern monarch population is declining (Brower et al. 2011; Rendón-Salinas and Tavera-Alonso 2013), and the advent of herbicide-tolerant crops and resultant loss

of milkweed in crop fields in the U.S. Upper Midwest has been identified as a possible primary threat contributing to this decline (Pleasants and Oberhauser 2012; Pleasants, this volume, Chapter 14); however, population surveys of migrating individuals in some locations do not show a similar downward trend (Davis 2011). To reconcile the conflicting patterns documented during different phases of their annual life cycle, and to identify critical phases in this cycle, we need to understand monarch population dynamics throughout the year.

To follow annual cycle dynamics, we divided the eastern monarch range into seven biologically relevant regions (Figure 24.1): overwintering sites, Texas Region, Southeast, Mid-central, Mid-east, North-central, Northeast. These regions were developed to reflect when and where activity is concentrated in each stage of the annual cycle, but we note that boundaries and seasonal definitions are approximations that can shift from year to year. For the analyses presented here, we focus on four regions and use the following abbreviations in figures and tables: OW (overwintering sites), TX (Texas), NCent (North-central), and NEast (Northeast).

We present the following simplified series of events (steps) throughout the monarch annual cycle to inform specific questions about monarch population dynamics (Figure 24.1). In Step 1, surviving monarch adults that arrived the previous fall leave their Mexican wintering sites in late February and early March, fly northward, and begin arriving in the Texas region in mid-March. Few individuals are observed north of 35°N latitude until several weeks later (Howard and Davis 2004), so we defined this latitude as the northern limit for spring breeding (Figure 24.1). We are less sure about the southern boundary of the spring breeding region because there are few spring observers in Mexico, but we assume that some egg laying occurs south of the U.S.-Mexico border. We also separated Florida, Georgia, and South Carolina into a separate region because individuals from the nonmigratory Florida population may fly north in the spring (Dockx 2012) and our work focuses only on the migratory population. For that reason, we tracked spring dynamics only in the Texas region. In Step 2, monarchs that migrated from Mexico lay eggs in the Texas region. This first pulse of egg laying and development continues until about early May (Prysbly and Oberhauser 2004) and produces that year's first generation of adults.

In Step 3, this first generation flies northward, with some individuals flying toward the North-central region and others toward the Northeast region (Steps 3a,b in Figure 24.1), in a split that is roughly around the Appalachian Mountains (Journey North 2013). Individuals usually arrive north of 40°N latitude by mid-May, but slightly later in the Northeast (Howard and Davis 2004). The northern boundary in Figure 24.1 is based on the northern limit of most observation records. In Step 4, monarchs produce two to three additional generations in the North-central and Northeast regions (Steps 4a,b in Figure 24.1) over a period of about three months, with first generation adults continuing to lay eggs until late June (MLMP 2013). Although some recruitment continues in all regions, we focus on the northern regions because there is little summer breeding south of our 40°N latitude cutoff (Prysbly and Oberhauser 2004, Baum and Mueller, this volume, Chapter 17) and because most individuals that migrate to the overwintering sites originate from the northern regions (Malcolm et al. 1993; Wassenaar and Hobson 1998).

In Step 5, most individuals enter reproductive diapause and migrate south. Although the timing varies by year and latitude, breeding generally winds down by mid- to late August in the northern regions (Prysbly and Oberhauser 2004; MLMP 2013). There appear to be fairly separate migrations from the Central and East regions (Calvert and Wagner 1999), with more sightings commonly reported in the Central region (Howard and Davis, this volume, Chapter 18). We know that egg laying occurs along the fall migratory pathway (Batalden and Oberhauser, this volume, Chapter 19; Baum and Mueller, this volume, Chapter 17), and it is unlikely that reproductive individuals fly all the way to the overwintering sites; however, because the vast majority of fall migrants are nonreproductive (Batalden and Oberhauser, this volume, Chapter 19), for the sake of simplicity we focus on the individuals that fly directly to the Mexican overwintering sites and ignore fall or winter reproduction in the United States. Individuals begin to arrive at the Mexican overwintering sites in early November, with stragglers arriving throughout November and probably into December (Rendón-Salinas, pers. observ.).

Step 6 represents winter survival. The individuals that arrive in the overwintering sites in late November remain there until they begin migrating north

again in February. To survive the winter, they must arrive with or obtain enough energy reserves to last the winter, survive any extreme weather conditions that occur, and avoid predation. Those that survive are part of the group that moves northward in the spring and begins the cycle again.

Here, we track year-to-year dynamics to determine the extent to which yearly variation in population size in one step explains yearly variation in the subsequent step. Specifically, a strong, positive relationship between steps suggests the number of individuals feeding into the next step has a strong influence on subsequent population size and indicates “carry-over” effects (Harrison et al. 2011). We do not include other potential explanatory factors in our models (e.g., climate, predator numbers, or resource availability); instead, we are simply attempting to determine the degree to which population dynamics at one stage are predictive of the next. The lack of a predictive link between steps could indicate that environmental factors (e.g., local climate) are swamping any carry-over effects; however, we are cautious about concluding that there is no link, especially when we observe nonsignificant trends or sample sizes are low. We have two reasons for our caution. First, there are steps for which we still have few data; second, citizen science data tend to be particularly variable for several reasons, including different skill levels, nonrandom placement of surveys, and irregular survey intervals. Low sample sizes and increased variability reduce statistical power; however, as data continue to accumulate, we will revisit these patterns to see whether suggested trends are supported or not. Further, as the data resources grow, power will increase to perform more sophisticated modeling that accounts for survey design and multiple interactions. For now, we offer a broad overview of the links between each step in the cycle by exploring the transitions (steps) illustrated in Figure 24.1 (note that we had insufficient data to explore Step 2):

- Step 1: Do the numbers of adults at the end of the winter in Mexico predict the number of adults recorded during the spring season in the Texas region?
- Step 3: Do numbers of adults (or their eggs) during the spring breeding season predict the numbers of first-generation adults (or their eggs) that arrive in the North-central or Northeast region?

- Step 4: Do the numbers of first-generation adults arriving in the north (or their eggs) predict how large the population grows during the summer in the North-central or Northeast region?
- Step 5: Does the size of the summer breeding population predict the number of fall migrants in the North-central or the Northeast regions or the size of the winter colonies soon after their arrival?
- Step 6: Does the size of the overwintering colonies in Mexico at the beginning of the winter season predict the size of the colonies at the end of the season?

METHODS

Continental-scale data from volunteer monitoring networks

A vast network of citizen science monitoring programs (Figure 24.2) covers the range of the eastern monarch, making this continental-scale, multi-year examination of monarch population dynamics possible. For these analyses, we used data from seven monitoring programs, briefly described below; full descriptions are given by Oberhauser et al. (this volume, Chapter 2).

Data on overwintering colony size in the Mexican Reserve (star in Figure 24.2) were provided by the World Wildlife Fund-Mexico (WWF) and Monarch Butterfly Biosphere Reserve (MBBR) personnel (Rendón-Salinas and Tavera-Alonso 2013). The area (combined across all sites) supporting roosting monarchs is calculated during 10 two-week periods throughout the season, starting in early November and going through late February; we used this area as a proxy for monarch abundance. For 1993–2003, only one estimate of the size of the arriving colony was made each year, but colony size estimates were made every two weeks throughout the winters of 2004–2011.

Data on relative adult population sizes in the spring and summer breeding grounds are provided by three general butterfly survey programs, the continental-scale North American Butterfly Association (NABA) Count Program (gray dots in Figure 24.2) and butterfly monitoring programs in Illinois (IL) and Ohio (OH) (black dots in Figure 24.2). The NABA program uses count circles of 25

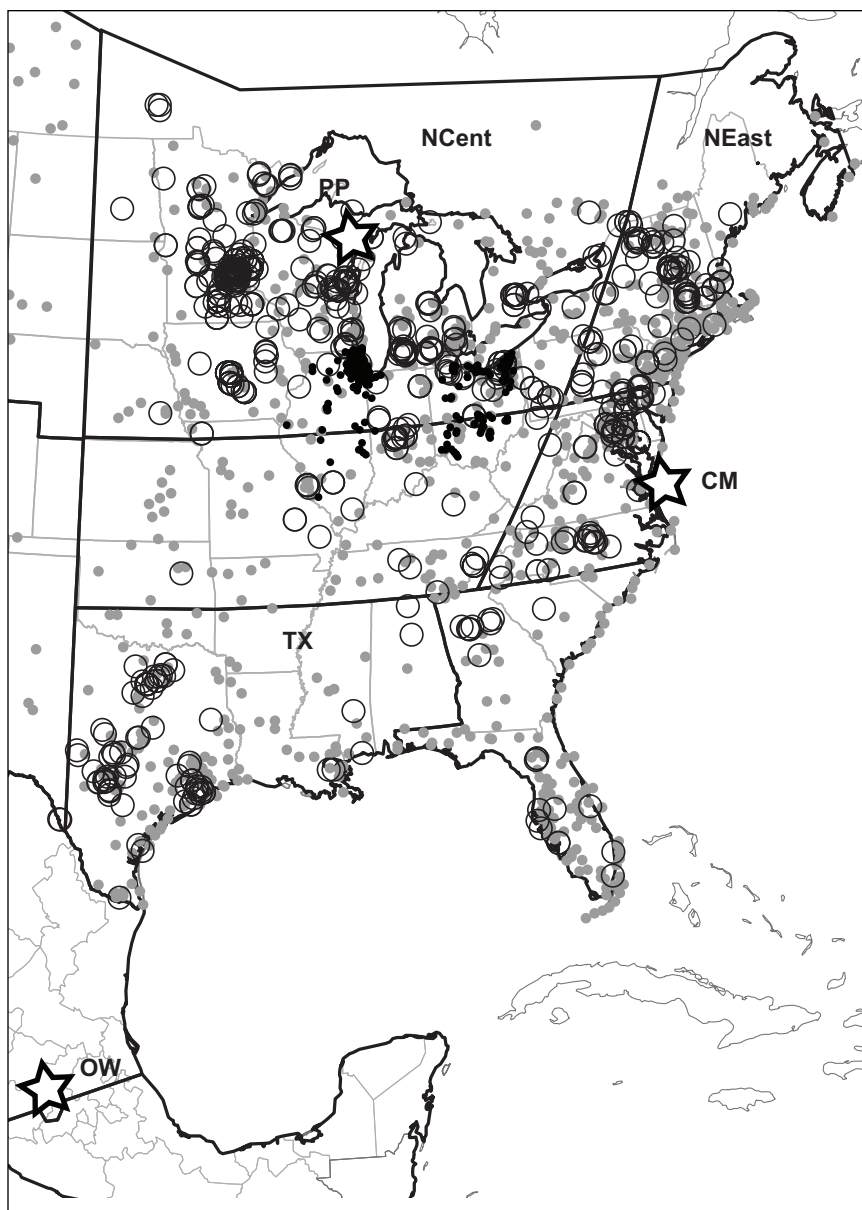


Figure 24.2. Sampling locations (2011 only) of 7 monitoring programs throughout eastern North America. Analyses are restricted to four focal regions: the North-central (NCent), Northeast (NEast), and Texas (TX) regions and the overwintering sites in Mexico (OW). During the spring and summer breeding seasons, adult monarchs are sampled by the North American Butterfly Association (gray dots), and by butterfly monitoring networks in Illinois and Ohio (black dots). Egg density is sampled by the Monarch Larva Monitoring Project (open, gray circles). Surveys of fall migrants occur in Peninsula Point MI (PP) and Cape May NJ (CM), locations shown with stars. A star also shows the location of the overwintering (OW) sites in Mexico.

km diameter in which groups of volunteers count all butterflies they see in a single day. We extracted monarch data and calculated the numbers of monarchs observed adjusted by the total number of hours spent by each group in the field for 1984–2011. In

the IL and OH programs, single volunteers walk set transects multiple times per year and record all butterflies observed. We extracted monarch records and calculated monarchs observed adjusted by the total number of hours spent on each transect. Data

from IL cover 1987–2011, and OH, 1996–2008. Values used for analysis were averaged within regions during each time period corresponding to the transitions explored for each step (Table 24.1).

We used egg densities recorded by the Monarch Larva Monitoring Project (MLMP) as a proxy for adult abundance. MLMP volunteers establish sites at milkweed patches, which they monitor weekly (open circles in Figure 24.2). They record the number of eggs observed each week, and the number of milkweed plants they search. We used per-plant egg densities that met certain screening criteria (see Pleasants and Oberhauser 2012). Because we do not account for milkweed abundance, egg densities will not correspond exactly to adult densities, especially when milkweed abundance varies from year to year. Data span 1997–2011. We averaged values used for analysis within regions during the time periods corresponding to each step (Table 24.1).

Indices of fall migration population abundance are taken from two locations that support consistent stopover sites from year to year (stars in Figure 24.2). Peninsula Point is on the southern shore of Michigan's Upper Peninsula. Cape May is also located on a peninsula at the southernmost point in New Jersey. Peninsulas often serve as funnel points on the southward journey and regularly host large populations (Meitner et al. 2004). These stopover sites are surveyed multiple times during the migration season, and we used the mean value across surveys for our analyses. We used data from 1996–2010 and 1992–2010 from Peninsula Point and Cape May, respectively.

Consistency between data sets

Although citizen science data often have large spatial and temporal coverage, they frequently do not use strict protocols, survey locations are not established randomly, and surveys may not be performed at the same time each year; nevertheless, they can provide robust data that allow many types of ecological and evolutionary questions at scales not possible from traditional academic surveys (Dickinson et al. 2012). Further, several studies have shown that overlapping bird monitoring programs tend to recover similar data patterns (e.g., Greenberg and Droege 1999; Lepage and Francis 2002; Link et al. 2006). Less comparison work has been done for butterflies (but see van Strien et al. 1997), but citizen

science monitoring data underlies much of what we know about butterfly responses to land-use and climate change in Europe (Settele et al. 2009) and examinations from two U.S. programs show that both are effective at capturing local community patterns (Matteson et al. 2012).

To test for consistency between data sets, we compared data from within the same region and season to determine whether we saw similar year-to-year trends. Here, the lack of a strong relationship among programs would indicate that the programs are not providing robust metrics of year-to-year patterns. This conclusion is distinct from conclusions we draw when testing for patterns across the steps in the annual cycle (the main focus of this chapter), where the presence or absence of a strong pattern is used to determine whether there are carry-over effects from one step to the next. To test for consistency, we used three data sets that measure adult densities (NABA, IL, OH) and one that measures egg densities (MLMP). Although variability in milkweed density may erode the relationship between adult and egg densities, we tested the utility of MLMP data as a proxy for adult numbers. We compared year-to-year densities for these four data sets during the North-central summer breeding season, calculating correlation coefficients for each comparison.

Abundances of adults as measured through the three monitoring programs were remarkably consistent (Figure 24.3), with high correlation coefficients that were statistically significant for all three comparisons, which is consistent with earlier results (Oberhauser 2007). As anticipated, egg densities correlated less closely with adult abundances. Still, the year-to-year trends showed similar patterns and all correlation coefficients were positive, although none statistically significant. Based on these results, we are confident that indices developed from adult data sets reflect relative abundances between years and seasons; however, because of lack of strong congruence between adult and egg data, we do not compare adult and egg data sets directly in any of our analyses.

Relationship between steps in the annual cycle

To explore population dynamics between transitions, we drew data from the monitoring data sets displayed in Figure 24.2. Although we have a tremendous amount of data, some region/season combinations have greater data availability than others.

Table 24.1. Analyses used to explore five of the six steps illustrated in Figure 24.1

St	Explanatory Variable				Response Variable				Results					
	Region	Date Range	Data (no. sites)	Region	Date Range	Data (no. sites)	N	Int	Slope	Sqr	LRT	adj P	R ²	Fig
1	OW	16–31 Jan	WWF (1)	TX	15 Mar–16 May	NABA (6)	7	0.70	0.14		0.42	0.32	0.20	–
3	TX	15 Mar–16 May	NABA (6)	NC	24 May–13 Jun	NABA (2.4)	7	0.27	0.55		0.27	1	0.09	–
3	TX	15 Mar–16 May	NABA (6)	NC	24 May–13 Jun	IL (55.9)	7	0.75	0.12		0.08	1	0.03	–
3	TX	15 Mar–16 May	NABA (6)	NE	24 May–4 Jul	NABA (17.7)	7	0.54	0.38		0.12	1	0.17	–
3	TX	15 Mar–16 May	MLMP (9.7)	NC	24 May–13 Jun	MLMP (44.5)	10	0.13	0.13		0.37	0.16	0.45	–
3	TX	15 Mar–16 May	MLMP (9.9)	NC	24 May–13 Jun	MLMP (42.8)	9	0.16	0.04		0.03	1	0.10	–
3	TX	15 Mar–16 May	MLMP (10.2)	NE	24 May–4 Jul	MLMP (11.4)	9	0.26	–0.09		0.85	1	0.05	–
4	NC	24 May–13 Jun	NABA (1.9)	NC	28 Jun–15 Aug	NABA (83.1)	16	1.73	2.68	–0.53	<0.01	0.001	0.68	24.4a
4	NE	24 May–4 Jul	NABA (15.1)	NE	5 Jul–15 Aug	NABA (41.6)	22	0.45	1.62		0.86	<0.001	0.53	24.4a
4	NC	24 May–13 Jun	IL (30.4)	NC	28 Jun–15 Aug	IL (65.8)	22	1.83	2.74		0.09	<0.001	0.58	–
4	NC	24 May–13 Jun	IL (31.2)	NC	28 Jun–15 Aug	IL (66.2)	21	1.42	3.46		0.65	<0.0001	0.76	24.4b
4	NC	24 May–13 Jun	OH (25.9)	NC	28 Jun–15 Aug	OH (27.4)	14	1.05	3.84		0.26	0.056	0.34	–
4	NC	24 May–13 Jun	OH (25.9)	NC	28 Jun–15 Aug	OH (26.8)	13	1.49	0.61		0.24	0.82	<0.01	24.4b
4	NC	24 May–13 Jun	MLMP (35.5)	NC	28 Jun–15 Aug	MLMP (51.1)	14	0.21	0.44		<0.05	0.1	0.48	–
4	NC	24 May–13 Jun	MLMP (33.6)	NC	28 Jun–15 Aug	MLMP (54.7)	13	0.13	0.95		0.95	0.02	0.52	24.4c
4	NE	24 May–4 Jul	MLMP (10.4)	NE	5 Jul–15 Aug	MLMP (16.3)	13	0.12	0.63		0.03	<0.01	0.81	–
4	NE	24 May–4 Jul	MLMP (8.6)	NE	5 Jul–15 Aug	MLMP (13.6)	12	0.07	1.86		0.35	0.0233	0.49	24.4c
5	NC	28 Jun–15 Aug	NABA (86.1)	NC	16 Aug–17 Oct	PP (1)	15	–32.18	46.30	–6.76	<0.01	0.03	0.56	24.5a
5	NE	5 Jul–15 Aug	NABA (44.2)	NE	16 Aug–17 Oct	CM (1)	19	5.01	14.79		0.90	0.04	0.41	24.5b
5	NC	28 Jun–15 Aug	IL (58.76)	NC	16 Aug–17 Oct	IL (18.6)	25	7.75	0.13		0.50	0.79	0.00	24.5c
5	NC	28 Jun–15 Aug	OH (29.5)	NC	16 Aug–17 Oct	OH (29.2)	13	1.87	1.27		0.41	0.32	0.17	24.5c
5	NC	28 Jun–15 Aug	IL (73.3)	OW	16–30 Nov	WWF (1)	19	13.60	–4.27	0.51	0.02	0.55	0.26	24.6a
5	NC	28 Jun–15 Aug	OH (29.5)	OW	16–30 Nov	WWF (1)	13	7.07	0.13		0.40	1	0.00	24.6b
5	NC	28 Jun–15 Aug	NABA (80.9)	OW	16–30 Nov	WWF (1)	19	7.59	–0.29		0.87	1	0.01	24.6c
5	NE	5 Jul–15 Aug	NABA (44.5)	OW	16–30 Nov	WWF (1)	19	7.00	–0.13		0.88	1	0.00	–
6	OW	16–30 Nov	WWF (1)	OW	16–31 Jan	WWF (1)	7	–0.81	0.87		0.55	0.01	0.74	24.7

Notes: Step number is shown in the right column. For each comparison, we performed ordinary linear regressions. The explanatory and response variable are shown separately in each row, including region (OW = overwinter sites, TX = Texas region, NC = North-central region, NE = Northeast region), date range, data source (WWF = World Wildlife Fund, NABA = North American Butterfly Association, MLMP = Monarch Larvae Monitoring Project, IL = Illinois, OH = Ohio) and the average number of sites (no. sites) over all years used in the analysis. The number of sites for the response variables were used as weighting factors. For each comparison, we show the intercept, slope, and, if appropriate, the square term from the model chosen (either linear or quadratic) by a likelihood ratio test. We present R^2 and P -values (adjusted using Holm-Bonferroni method to account for multiple comparisons within each question) to illustrate the fit of models. If a significant result was achieved, but a single point had excessive leverage (Cook's D score > 1), that point was dropped from the analysis and a new analysis conducted, shown below shaded in gray. For results illustrated in figures, the figure number is shown; points identified as outliers are circled within those figures.

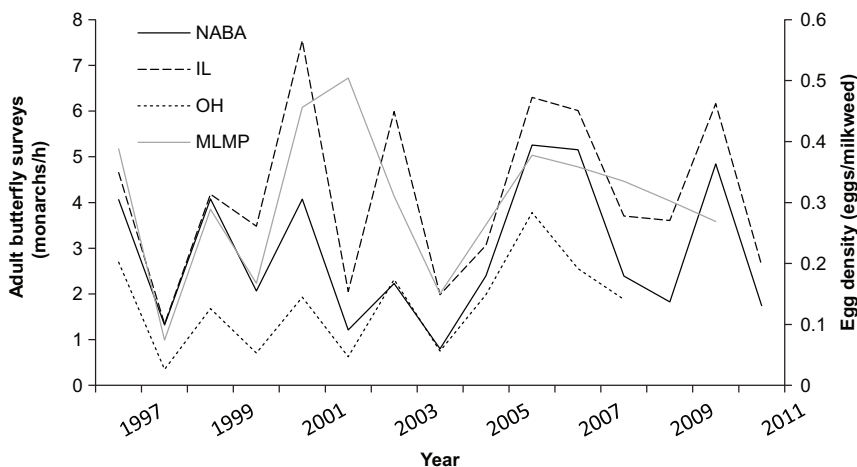


Figure 24.3. Similar year-to-year trends recorded by programs estimating monarch abundance during the summer breeding season in the North-central region. Pearson's correlation coefficients between programs: NABA and OH ($R^2 = 0.69^{**}$), NABA and IL ($R^2 = 0.68^{**}$), OH and IL ($R^2 = 0.68$). * $P < 0.05$, ** $P < 0.01$, all P -values calculated with a sequential Bonferroni correction (Holm 1979). None of the comparisons with MLMP data were significant, but all had positive correlation coefficients (MLMP and NABA, IL, and OH $R^2 = 0.40, 0.49, 0.50$, and Bonferroni-corrected P -values = 0.20, 0.20, and 0.10, respectively).

NABA and MLMP, the only programs that cover the entire breeding range, have more summer than spring and fall data, limiting our power to test spring or fall linkages with data from those programs. We have more data throughout the full season from the IL and OH butterfly monitoring networks, although these programs allow explorations only in the North-central region. We parsed the region and date ranges for exploring each question based largely on the timeline of events described above, but also adjusted to decrease overlap between generations and for general data availability. We performed ordinary linear regressions where the predictor variable was always the abundance index of the earlier step and the response variable the abundance measured in the subsequent step. Multiple comparisons were possible for most steps (Table 24.1).

We developed a monarch abundance index for each monitoring program (see program descriptions above) and calculated its value for each year/region/season combination. Although for the purposes of analysis, each year/region/season index contributes one data point to the analysis, each point is actually based on multiple surveys within a region. For example, if we compare trends over 10 years, the sample size for our regression test will be 10, but data for each point will be drawn from multiple survey sites, sometimes numbering in the dozens (Figure 24.2).

Table 24.1 shows the average number of sites, over all years, available for each abundance index we calculated. Further, except for the NABA counts, all sites have multiple surveys performed during the year, and those numbers are pooled for each site and specified data ranges within years. We used the number of sites underlying the response data as a weighting factor in each analysis, and we performed analyses only when we had at least five years of data.

Earlier exploratory analysis suggested that some relationships might be curvilinear, so we ran each model both including and excluding a squared term. We used a likelihood ratio test to choose between the linear and quadratic models (Table 24.1). We also present the R^2 and P -values for the best model to illustrate the strength of fit. P -values were adjusted using a sequential Bonferroni correction (Holm 1979) when there were multiple comparisons within a step. Whenever we had multiple tests examining the same step, we always considered whether there was a dominating pattern in the multiple tests, especially when there were conflicting results or non-significant trends. As noted earlier, observed trends can easily be retested as more data become available. To consider the possible influence of outliers, we calculated a measure of Cook's Distance and identified any data points with a value greater than 1 as outliers (Cook and Weisberg 1982) and we present

results with and without these outliers. Analyses from which outliers were removed are highlighted in gray in Table 24.1 and are always shown beneath the model with all data included. All analyses were done in R 2.15.2 (R Core Team 2012) using the *lm* procedure. Likelihood ratio test results were generated using the *lmtest* package (Horthorn et al. 2013).

The transition between the arrival of migratory individuals from Mexico and the first generation of the year is Step 2 in Figure 24. 1. We had insufficient early and late spring data to analyze this step. Further, to explore patterns within Steps 1 (relationship between winter numbers and Texas arrivals) and 3 (relationship between first-generation adults and arrivals in the north), it would be ideal to separate adult data for the spring breeding season into an early (arrivals) and late (first-generation recruits) period; however, we lacked enough NABA spring data in TX to allow this separation. Therefore, we used an index of the entire spring generation time for both questions, assuming that numbers across the entire season reflect both arrivals and the amount of recruitment. For Step 3, only 4 years of overlap occurred between WWF and OH data, which did not meet our 5-year minimum criterion. For Step 4, we used NABA and MLMP data to compare within-region abundance indices for the spring and summer in the North-central and Northeast regions. We used IL and OH butterfly monitoring network data to perform additional analyses on the same question in the North-central region only.

We examined two points along the pathway of Step 5 (migration from summer breeding to the overwintering sites, Figure 24.1). First, we compared late summer numbers to fall migration abundances using Cape May and Peninsula Point data (first two rows for Step 5 in Table 24.1). Note that only Cape May occurs south of the region that is the source of migrating adults, while Peninsula Point is closer to the northern limit of adult activity. Since monarchs are migrating south, we have an a priori expectation that comparisons using Cape May data (Northeast region) will provide a better test than Peninsula Point (North-central region). Nevertheless, we present comparisons from both sites. We also present comparisons between IL and OH summer and fall indices to explore this segment of Step 5 (third and fourth rows for Step 5 in Table 24.1), but cannot use NABA data since there are too few fall counts. However, the key comparison for Step 5 is determin-

ing the success of the end-of-summer population at making it to the overwintering grounds in Mexico; therefore, in a second set of comparisons for Step 5, we compared end-of-summer adult numbers (NABA, IL, OH) with colony size in Mexico during the two-week arrival period at the end of November (fifth through eighth rows for Step 5 in Table 24.1).

To explore Step 6, overwintering survival in Mexico (Figure 24.1), we compared WWF monitoring data from the beginning and end of the season. In addition to quantifying the relationship, by comparing final overwinter size to a 1:1 line indicating no mortality, we are able to estimate overwintering mortality.

RESULTS

Results are shown for all comparisons in Table 24.1 with the focal Step indicated in the first column. For each comparison, the data sets and date ranges used for each test are shown along with sample sizes. Here, sample size is the number of years of data available for comparison (n), but we also note the average number of sites that contributed to each year's single datum. Recall that for each site, there are also multiple surveys done within the season (except for NABA), but these numbers are not shown. Parameter estimates from either the linear or quadratic models are shown depending on the likelihood ratio test, and the R^2 and adjusted P -values are also shown for each comparison. Slope and intercept estimates are shown for all models and the square term only if the quadratic was the chosen model.

There are few spring surveys for any of the monitoring programs, so comparisons that include the spring stage (Steps 1 and 3) have data only from 7–10 years and those data points are estimated from only 6–10 individual sites on average (Table 24.1). There was only one comparison possible to test the relationship between late winter colony size and the spring population in the Texas region (Step 1). A positive slope suggests there may be a relationship (figure not shown), but at this point there are too few years of data based on too few sites for a robust test. For Step 3, we were able to make multiple comparisons to test the relationship between spring migrants in TX and spring arrivals in the North-central and Northeast regions; none were significant (but 5 of 6 had positive slopes). The only comparison that even

approached significance was that between egg densities in Texas and North-central regions, but when an identified outlier was removed, the relationship disappeared entirely (Table 24.1).

Although we have very few survey data tracking dynamics during the spring growing season in the South, both the IL and OH data sets provide substantial data on spring arrivals in the North. Surveys for these programs begin in spring, and any monarchs observed in early May are almost exclusively adults that were recruited further south in the spring. Therefore, we had the most data available to compare spring arrivals in the north with the size of the summer breeding population (Step 4). In the North-central region, we compared four data sets (NABA, IL, OH, MLMP) at the beginning and end of the breeding season, and in the North-east we compared NABA and MLMP. All comparisons were highly or nearly significant, even with the Bonferroni correction (Table 24.1), and all showed a positive relationship (Figure 24.4). Removing outliers caused only one relationship to lose significance (OH).

We found mixed results when examining the first segment of Step 5, population size at the end of the summer and abundance of fall migrants. In the Northeast region, there was a positive relationship between summer numbers and fall counts at Cape May (Table 24.1 and Figure 24.5a); however, there was an unexpected parabolic relationship between summer adult populations in the North-central region and stop over sizes at Peninsula Point (Figure 24.5b). We again note that the subregion funneling into Peninsula Point is largely unmeasured. Interestingly, there was no significant relationship between summer and fall population sizes within the IL or OH data sets (Table 24.1, Figure 24.5c).

For the full journey illustrated in Step 5 (North-east and North-central to overwinter sites in Mexico, Figure 24.1), we found no significant relationships between summer (NABA, IL, OH) population indices and the size of the arriving population in Mexico, suggesting a disconnect between the summer and overwinter numbers; however, although no data points were identified as outliers using the Cook's D test, visual examination suggests two outliers (circled in Figure 24.6). A relationship is suggested if those outliers are removed, and this relationship should continue to be examined as more data become available. Finally, for the seven years of data we had available, there was a strong relationship between the

colony size at the beginning and end of winter (Table 24.1, Figure 24.7). The points lie close to the 1:1 line, suggesting that for the seven years for which we have data, little overwinter mortality occurred; we note, however, that this interpretation of the data assumes that monarch densities within the measured colony areas are the same at the beginning and end of the winter, which may not be the case.

DISCUSSION

Our step-by-step analysis of the annual cycle of eastern monarchs suggests that the most critical factor impacting the size of each year's breeding population appears to be the size of the first generation of migrants that arrives each year in the north. In both the North-central and Northeast regions, the number of individuals arriving was highly predictive of the eventual size of that summer's population (Step 4), whether we looked at adult or egg density data (Figure 24.4). This suggests that previous transitions that determine the number of monarchs arriving in the north are crucial, and that factors that occur over the course of the summer are less important in driving population, at least during the years for which we had data. However, because we lack sufficient data on dynamics during the spring recruitment and subsequent migration period, it is impossible to say if the crucial step driving that result is the number of spring arrivals from Mexico (Step 1), spring recruitment (Step 2), or successful northward migration of the first generation of adults (Step 3). Recent modeling showed that temperature and precipitation in Texas during the spring had a stronger impact on summer monarch population growth in Ohio than did temperature and precipitation during the summer (Zipkin et al. 2012); however, it is important to note that while the Zipkin et al. model suggests that spring recruitment (our Step 2) is one important driver, it does not address the potential contributions of Steps 1 or 3. A focus of future research should be teasing apart the contributions of these early stages on the number of arrivals in the Northeast and North-central regions.

We were able to provide preliminary explorations of patterns for Steps 1 and 3 (no data for Step 2 were available). No significant relationship was found between the area occupied by adult monarchs at the end of the overwintering period in Mexico and

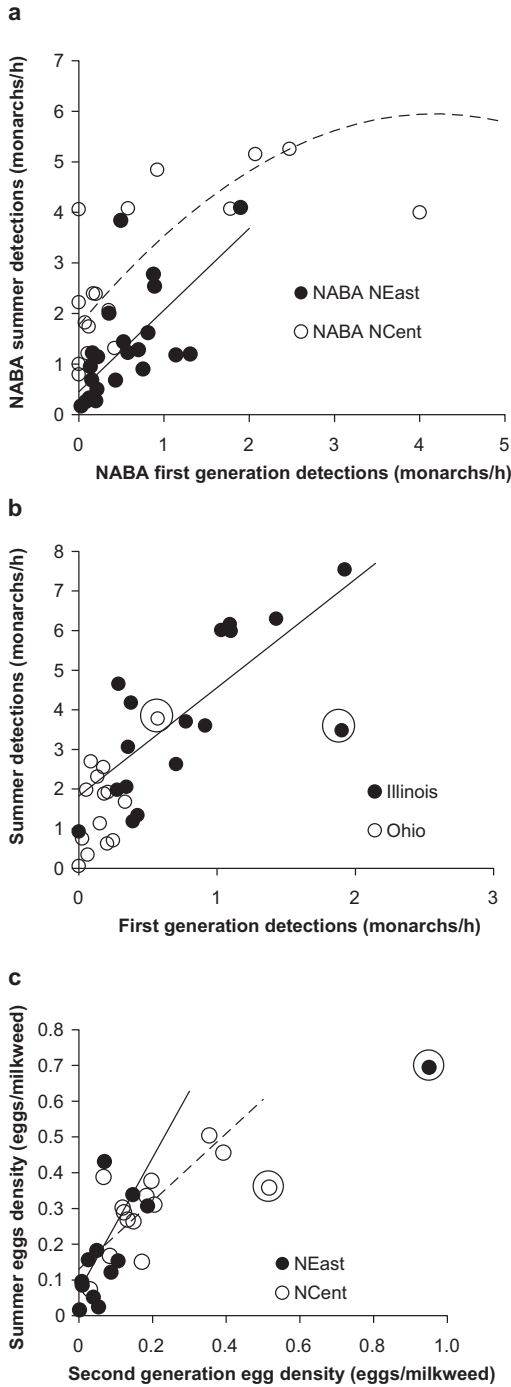


Figure 24.4. Three relationships between adult arrivals or egg density in the north at beginning of season compared with population sizes at end of season: (a) NABA data in the NEast and NCent regions, (b) Illinois and Ohio data in the NCent region, and (c) MLMP egg data in the NEast and NCent regions. In all panels, dashed lines indicate models fit to white dots and solid lines indicate models fit to black dots. Model parameters and significance levels in Table 24.1 are presented with and without the outliers that are circled here. Outliers are excluded from model fits presented in the figure.

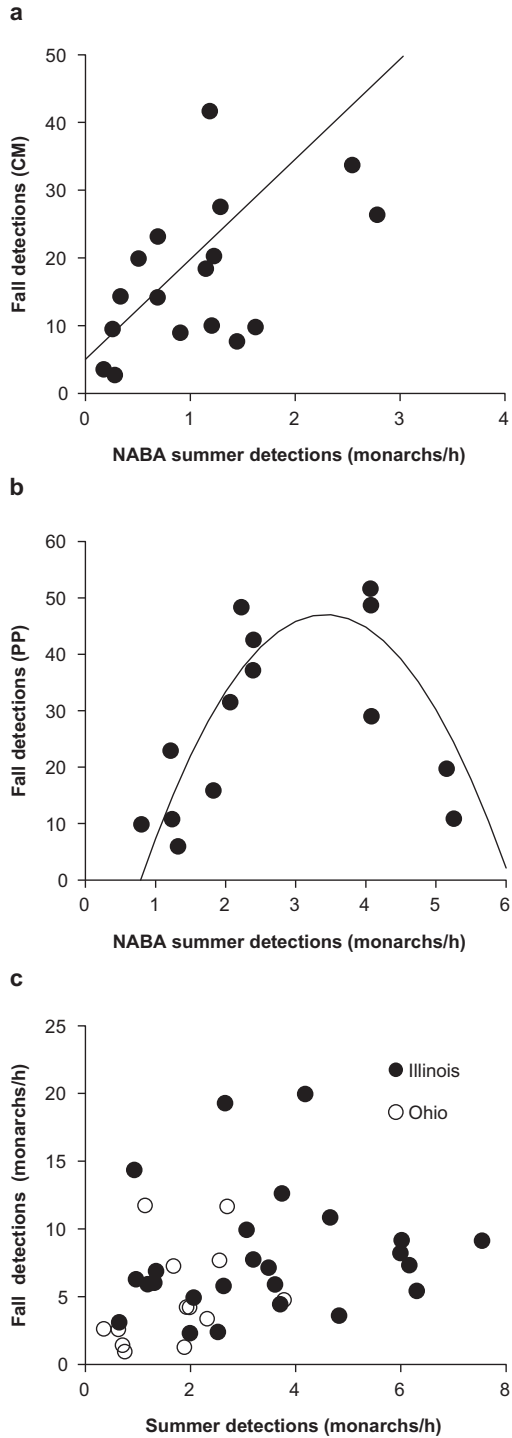


Figure 24.5. Relationships between summer adult detections and fall migration numbers. The relationship between NABA counts and the two fixed stopover site surveys, (a) Cape May and (b) Peninsula Point, showed significant relationships, but no relationship was found between late summer and fall detections in (c) IL or OH. Model parameters and significance levels shown in Table 24.1.

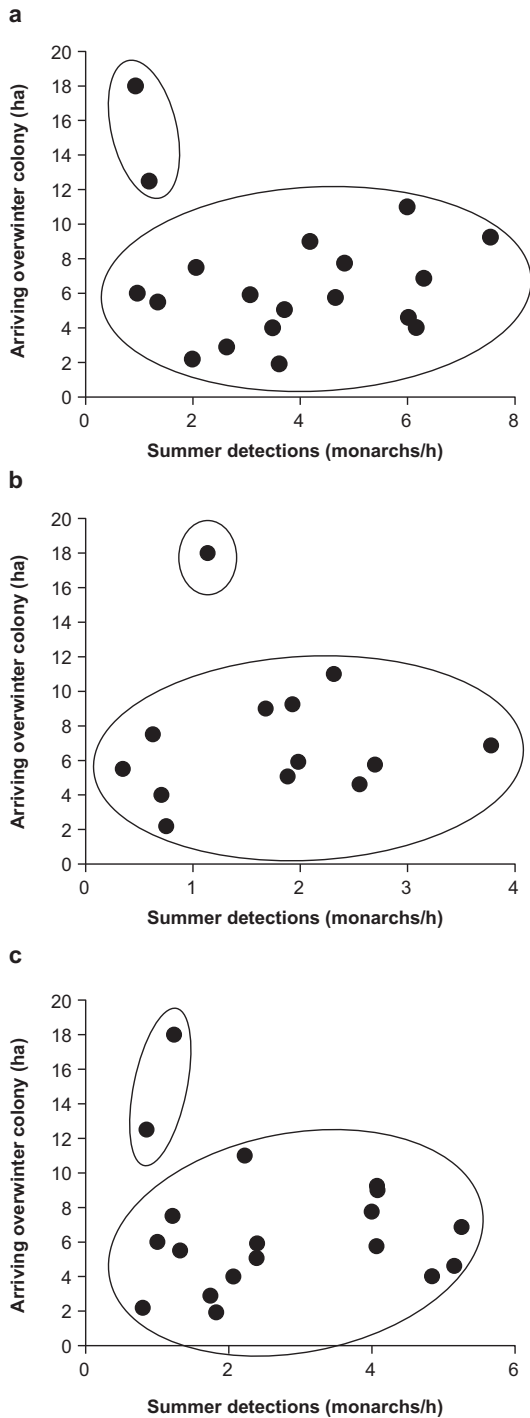


Figure 24.6. Relationships between end-of-summer adult detections in the NCent region and colony size at the beginning of the overwinter period from (a) Illinois, (b) Ohio, and (c) NABA. None of these relationships are significant, even if the outliers are removed, but still suggest a relationship that should be re-examined as more data become available.

the numbers of adults arriving in the Texas region (Step 1); however, it is important to note that we had only one data set (NABA) to compare with colony size data from Mexico, data were available from both sources during only seven years, and NABA data were based on very few surveys (Table 24.1). A positive relationship is suggested, and it will be valuable to continue to track this transition. If the lack of a relationship holds, it suggests that environmental conditions during the northward migration through Mexico swamp the relationship between numbers leaving the wintering sites and entering the Texas region, and thus that this is a crucial transition for monarchs. Increased monitoring throughout the spring migration is essential to do a better job of quantifying this relationship and determining the important drivers during this critical phase.

There was also no significant relationship between the number of monarchs observed in the Texas region in the spring and the number of first-generation individuals in the north (Step 3). In fact, the only comparison showing a trend (MLMP in the Texas region compared with MLMP in the North-central region) was lost when an outlier was removed. It is possible that these results are simply a detection problem resulting from the relatively small number of spring surveys on which the yearly indices are based; it is important to note that five of six comparisons had positive trends (Table 24.1). Further, as noted earlier, we had insufficient data to divide the spring population into early arrivals

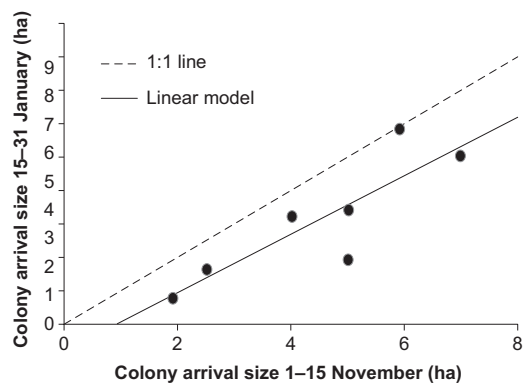


Figure 24.7. Relationship between colony size at the beginning and end of winter at the overwinter sites (solid line, $y = 6.1901x - 0.8091$). Because there is no recruitment during the winter but always mortality, the numbers at the end of the winter should always be lower, so points are a priori expected to fall below the 1:1 line (dashed line).

and the population size after spring recruitment. Using population numbers from late in the spring would be the most rigorous approach to exploring this question and enable us to capture the impact of spring weather on spring recruitment, which has been shown to be important (Zipkin et al. 2012). Ultimately, until we have more spring data, it will be difficult to have enough power to test this question rigorously. Further, if data were sufficient to split between early and late spring numbers, we could address population growth during the spring (Step 2 in Figure 24.1). Increased spring monitoring in the south would greatly enhance our ability to explore dynamics during this phase; more structured surveys of adults (repeated surveys at the same sites accounting for effort, such as those done by NABA, IL, and OH) would allow us to assess both the size of population arriving from Mexico and numbers of their adult offspring, which migrate northward.

Numbers at the end of the breeding season appear to have variable relationships with numbers observed during the fall (first segment of Step 5). Ideally, late summer population observations should be made north of fall migratory stopover sites with which they will be compared. We were able to do this only for the comparison between late summer observations in the Northeast and those in Cape May, and found a positive relationship (Figure 24.5a). We do not see that relationship when making the same comparison at Peninsula Point, possibly because this count measures butterflies that have flown from more northerly regions. We also saw no pattern when comparing late summer OH and IL counts with fall OH and IL counts; however, fall counts in OH and IL probably include migrants from further north, and thus might not reflect local summer abundances. Detection dynamics may also be a factor here since migrating monarchs tend to come in spurts and cluster in overnight roosting locations, meaning they are both temporally and spatially clumped during the fall and thus more difficult to detect. We may need to use more sophisticated modeling to explore this relationship more rigorously. We have no explanation for the parabolic shape of the relationship between North-central and Peninsula Point (Figure 24.5b) and suspect this may be spurious, but as we continue to accumulate monitoring data we will be able to determine whether that unexpected pattern holds.

There were also no significant relationships between late summer (NABA, IL, OH) population

indices and the size of the wintering population (the full pathway of Step 5) despite the fact that we have a great deal of data available to develop end-of-summer abundance indices. This lack of relationship suggests that variable migration success may be a key driver of observed patterns, or that other factors, such as breeding habitat loss (Pleasants and Oberhauser 2012; Pleasants, this volume, Chapter 14), are swamping our ability to detect the relationships. Brower et al. (this volume, Chapter 10) suggest that fall nectar availability is important to migratory success, and it is likely that this availability varies from year to year. Another large unknown is the proportion of individuals that remain in the southern United States (Batalden and Oberhauser, this volume, Chapter 19) and whether this varies from year to year. Finally, our late summer and fall abundance indices measure local densities, while the measurements in Mexico measure the entire population. Overwintering colony size has declined over the past several years (Brower et al. 2011; Rendón-Salinas and Tavera-Alonso 2013), yet summer counts do not reflect that, nor do patterns at fall stopover sites (Davis 2011). Trying to pin down the causes of this mismatch, if it holds with more data, should be a focus of future research because it suggests that fall migration is a key stage in the annual cycle.

The strong relationship between early and late winter population size suggests that overwintering mortality generally is not variable enough to erode the relationship between how many monarchs arrive and how many are alive at the end of each winter. Further, for the seven years we examined, overall mortality appeared to be low since observed values fell close to the 1:1 line (Figure 24.7). It is important to note, however, that none of the years included in this analysis had a catastrophic mortality event, which happens periodically (Brower et al. 2004).

Our results highlight (1) steps that appear to be critical and thus important for conservation focus, but that are also understudied, and (2) critical steps that should be the focus of more sophisticated modeling. These points are well illustrated by our results focused on dynamics in the spring. Numbers arriving in the northern United States are critical to the size of the breeding population for the rest of the summer (Figure 24.4), and previous models (Zipkin et al. 2012) show that Texas climate in the spring has the strongest influence on summer growth, yet we do not know the extent to which each of the earlier

steps influences those numbers. Another critical step highlighted by this analysis appears to be the fall migration (Step 5), illustrated by the disconnect between population trends in the summer and winter stages. Understanding the lack of a significant relationship between summer numbers and winter colony size, and the role of events during the migration, should be a focus of future research. This relationship will be easier to understand as more data accumulate, but more sophisticated modeling will be required to tease apart potential interacting factors.

Our analyses also highlight the value of the citizen science programs that provided the data. Not only do the results show that valuable and consistent information is contained within the data (Figure 24.3), but they also highlight the spatial and temporal scales over which we can now ask (and answer) questions. The fact that these data continually stream in each year means that we will be able to reexamine our results, especially those for which we had too little data to rigorously explore in this analysis (Steps 1, 2, and 3). While we were fortunate to have anywhere from 7 to 22 years of data with which to explore our questions (Table 24.1), those years are still a sample of the different combination of factors that could arise to impact population dynamics. For example, this work, as well as that of previous modeling efforts (Zipkin et al. 2012), suggests that conditions during the summer are not as critical as the spring for growth; however, in 2012, which was not included in any of our analyses, spring conditions may have been conducive for growth, yet record summer temperatures and a severe drought in the Upper Midwest likely had a negative impact on the year's population, and the arriving population in Mexico

was the lowest ever at that time (Rendón-Salinas and Tavera-Alonso 2013). As the climate changes, we need to constantly examine and reexamine the critical transitions between each region and stage; these continuing investigations can only be done thanks to the hard work and dedication of thousands of citizen science volunteers.

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