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Temporal and Geographic Variation in Monarch Densities: Citizen Scientists Document Monarch Population Patterns

Michelle D. Prysby and Karen S. Oberhauser

INTRODUCTION

Few long-term records of insect populations exist, especially for nonpest species (Varley et al. 1974; Price 1984). Long-term data on abundance can help us better understand the ecology of insect populations and the impact of global climate change, pollution, habitat destruction, and other anthropogenic factors on them (e.g., Ehrlich and Murphy 1987; Pollard and Yates 1993). Monarch butterflies are especially interesting candidates for long-term population studies because of their continent-wide distribution, multiple overlapping generations, and annual long-distance migration. In addition, such studies will help us to understand the effects of anthropogenic practices such as pesticide use and habitat destruction, to identify and understand sources of variation in monarch abundance, and to identify regions or habitats of special importance to the production and recruitment of monarchs. Participants in the 1997 North American Conference on the Monarch Butterfly identified several research priorities to address these needs, including monitoring the distribution and abundance of monarchs, studying environmental effects on their distribution and abundance, and studying sources of mortality during all monarch life stages (United States Fish and Wildlife Service 1999).

Several programs monitor adult monarch populations. The North American Butterfly Association's annual Fourth of July Butterfly Count monitors summer populations (Swengel 1995); the Monarch Monitoring Project at Cape May Point, New Jersey, and Texas Monarch Watch monitor the size and timing of autumn monarch migrations (Walton and Brower 1996; Calvert and Wagner 1999); the Journey North program monitors the timing of the spring migration (Donnelly 1999; Howard and Davis, this volume); and researchers in Mexico monitor the size of the overwintering monarch colonies (García-Serrano and Alvarez 1999; García-Serrano et al., this volume). Missing in this array of programs is a study of monarch egg and larval populations. By monitoring immature stages, we can measure the temporal and spatial variation in monarch reproduction and learn more about how monarchs use the available habitat. We can also compare population statistics on immature stages to those estimated for summer, fall, and winter adult populations to identify how population size at one stage affects that at later stages.

Relevant monarch biology

The breeding range of the eastern migratory population (the focus of this study) extends from the southern United States to southern Canada and from the Atlantic Seaboard to the Rocky Mountains. The range is limited by the range of the monarch's host plants, which are all in the Asclepiadaceae family and primarily in the genus *Asclepias* (Lynch and Martin 1993). Each spring, the migratory generation returns to the southern United States from central Mexico and lays eggs. Successive generations recolonize the rest of the summer breeding range (Cockrell et al. 1993; Malcolm et al. 1993; Howard and Davis, this volume). Monarchs appear to vacate the southern United States for much of the summer, probably owing to high temperatures and host plant dieback (Malcolm et al. 1987; Calvert 1999). There is some evidence for more fall breeding in the southern United States (see Results), but it is unknown whether these reproductive butterflies are migrants returning from the north or butterflies that have remained in the south for the summer by utilizing nonnative *Asclepias curassavica* plants, or whether these fall offspring join the southern migration (Calvert 1999).

Monarchs have five larval instars. Under typical spring temperatures at 45° north latitude, development can require more than 60 days, compared to fewer than 30 days under summer conditions (Cockrell et al. 1993).

Interannual and geographic variation in monarch abundance

There is considerable evidence for yearly variations in monarch abundance throughout the annual cycle (Swengel 1990, 1995; García-Serrano and others 1999, this volume; Monarch Monitoring Project 2002). Possible causes include variation in abiotic factors (temperature, humidity, precipitation, and storm events), natural enemy abundance, host plant availability or quality, and human activities such as pesticide use and habitat destruction. Both the Fourth of July Butterfly Count data and the Cape May data illustrate a large drop in the number of monarchs between 1991 and 1992, and Swengel (1995) and Walton and Brower (1996) implicate abiotic factors in this decline. Zalucki and Rochester (1999) modeled the effects of climate on annual abundance of monarchs in Australia, finding that monarch abundance theoretically could vary among years by as much as 500%, due solely to weather-related abiotic factors.

Similarly, counts of adult monarch butterflies indicate a geographic variation in abundance. Counts appear to be lower in the eastern United States than in the Midwest (Malcolm et al. 1993; Swengel 1995; Calvert and Wagner 1999). Malcolm and coauthors (1993) argue that most monarchs migrate north through Texas and continue on to the Midwest and Great Lakes region, while a smaller number continue to the Northeast region. In addition, Wassenaar and Hobson (1998) used stable isotope analysis to identify the natal origins of monarchs at the Mexican overwintering sites, and found that 50% of these butterflies originated in the midwestern United States.

Variation in monarch phenology and within-year abundance patterns

There is general agreement that monarchs produce three generations in the northern part of their range. This estimate is supported by models that consider the number of day-degrees achieved for various sites (Malcolm et al. 1987) and by empirical evidence (Borkin 1982).

Both Cockrell and coworkers (1993) and Journey North (2002a) show significant variation among years in the onset of monarch reproduction in the Upper Midwest. Journey North data indicate that the dates of monarch arrival in Minnesota and Wisconsin can vary by several weeks, and that 1997 was a particularly late year (Journey North 2002b). This variation is expected, since the arrival of monarchs in the Upper Midwest depends on the timing of departure from the overwintering sites, the rate of development for the southern generations, and prevailing weather conditions along the migration routes, all of which may vary significantly among years. The end of reproduction, however, appears to be more consistent. By the last week in August, one third of wild-caught female monarchs in west-central Wisconsin and east-central Minnesota are in reproductive diapause, as are half of female monarchs emerging in outdoor cages during the last week of August (Goehring and Oberhauser 2002), presumably in response to changing daylength and temperature conditions. By the end of the second week in September, all wild-caught and emerging captive female monarchs are in diapause (Goehring and Oberhauser 2002).

Estimates of and variation in monarch survival

Monarchs experience high mortality rates in the early immature stages, following a typical type A survivorship curve (Zalucki and Kitching 1982). Four studies that reported mortality rates for naturally occurring monarchs produced similar mortality estimates. In Australia, Zalucki and Kitching (1982) observed 2% to 8% survival rates between the egg and fifth instar (L5) stages. In Wisconsin, Borkin (1982) estimated a 12% survival rate from egg to pupation. In Louisiana, Lynch and Martin (1993) observed a survival rate of 4% from egg to L5, and

Oberhauser and colleagues (2001) estimated approximately 5% to 10% survival rates from egg to L5 for sites throughout the breeding range. Zalucki and Kitching (1982), Lynch and Martin (1993), and Oberhauser and colleagues (2001) all found that most mortality occurred by the L3 stage. Little research exists on temporal, geographic, or habitat-based variation in mortality, although there is some evidence for increasing mortality with increasing size of milkweed patches (Zalucki and Kitching 1982).

The Monarch Larva Monitoring Project

The Monarch Larva Monitoring Project (MLMP) (Prysby and Oberhauser 1999) was designed to describe temporal and geographic variations in monarch egg and larval abundances, compare monarch production across different habitat types, and describe variations in monarch egg and larval survival. In order to gather data to describe these variations on a large scale, we relied on citizen science methods. The term "citizen science" refers to the involvement of nonscientists in scientific research. We used citizen science methods to allow us to obtain monarch population data over wide spatial and temporal scales and to promote public understanding of monarch ecology and conservation and of scientific research. Citizens have a long history of involvement with monarch research, beginning with Fred Urquhart's monarch tagging program in 1952 (Urquhart 1960) and continuing with programs such as Monarch Watch, Journey North, and Texas Monarch Watch. Since citizens have played a critical role in obtaining the knowledge that we have about monarch populations, their involvement should be incorporated into new monitoring projects whenever possible.

Here we describe MLMP methods and summarize the findings to date. These first in-depth analyses focus on phenological patterns in oviposition, and variations in abundance and survival. Data on parasitism rates are presented by Prysby (this volume).

METHODS

Volunteer recruitment and training

Volunteers were recruited via Monarch Watch (Monarch Watch 2002) and Journey North (Journey North 2002b) listservs, the Monarch Lab and MLMP websites (Monarch Lab 2002; Monarch Larva Monitoring Project 2002), word of mouth, and a network of cooperating nature centers. Many teacher-participants were part of the Monarch Monitoring Project, a program co-sponsored by Monarchs in the Classroom and the Science Museum of Minnesota and funded by the National Science Foundation.

Volunteers received hard copies of instructions or read them on our website, participated in 4- to 11-h workshops at nature centers, or were trained during the teacher Monarch Monitoring Project. Training workshops at nature centers were held in 1999 and 2000 in Tennessee, Vermont, and Wisconsin. In 2002, we instituted a series of 1.5-day train-the-trainer workshops for naturalists, with the first four presented in Minnesota, Vermont, North Carolina, and Texas. Naturalists then conducted their own 4- to 6-h sessions. Workshops consisted, at minimum, of a slide presentation on the biology and ecology of the monarch butterfly, a hands-on activity to learn to recognize its life cycle stages, practice with the monitoring protocol in the field, and a question-and-answer period.

We communicated with volunteers through e-mail, mailings, and the MLMP website. Mass communications included reminders to start monitoring and send in data, thank-you notes, informal questionnaires, and an annual newsletter. We also corresponded with individual volunteers in response to specific questions.

Scientist involvement

Scientists and field assistants from the University of Minnesota monarch lab group monitored a field site in west-central Wisconsin, using the same methods as the volunteer participants. In addition, three teams of collaborating scientists in Ontario, Iowa, and Maryland joined us in a more controlled study funded by the U.S. Department of Agriculture (USDA) to compare the abundance and survival of monarchs in cornfield, edge, and nonagricultural habitats (Oberhauser et al. 2001). The study used methods similar to those of the volunteer program with adaptations for agricultural habitats, and these results are included in the monitoring database.

Monitoring protocol

Each volunteer chose a site containing milkweed to monitor on a weekly basis. The number of milkweed ramets (individual stems that may be connected by roots to a larger plant), site size and type, and site location had no minimum requirements and varied greatly. Sites included small backyard gardens, railroad right-of-ways, abandoned fields and pastures, and restored prairies. Volunteers recorded the location, type, and dimensions of the site, and milkweed species and density. Those with small sites recorded the total number of milkweed ramets in the site along with the area of the site, and those with larger sites counted ramets in 15- to 100-m^2 plots along belt transects.

Volunteers estimated the monarch densities per ramet each week. They either examined all of the milkweed ramets in smaller sites or sampled a subset of ramets in larger sites. Participants who sampled a subset of ramets used haphazardly placed belt transects, thus avoiding the bias that could result from selecting ramets that might be more likely to have monarchs on them. They recorded the number of eggs and larvae (identified to instar) observed and the number of ramets examined. Larval instars were identified by head capsule size and tentacle length, following Oberhauser and Kuda (1997). Resulting data were summarized as number of monarch eggs and larvae per ramet.

Many volunteers monitored the characteristics of the milkweed ramets. They observed a random sample of ramets at evenly spaced intervals along a haphazardly placed transect, recording ramet height; presence or absence of buds, flowers, and seed pods; descriptions of any invertebrates observed on the ramet; leaf condition; and damage from herbivory or disease. Finally, they measured milkweed density within 1 m^2 of the focal ramet. They made the same measurements for all milkweed ramets with monarchs on them, thus providing records of the characteristics of "average" milkweed ramets and ramets with monarchs on them. These data have not been analyzed to date.

Approximately 10% of the volunteers collected fourth and fifth instar larvae found at the site and reared them to estimate rates of parasitism by flies and wasps. They recorded the date and larval stage at the time of collection and the outcome (healthy adult, parasitized by fly, parasitized by wasp, or died of unknown cause). The protocol directions included characteristics of common fly and wasp parasitoids, and volunteers only needed to identify the parasitoid to taxonomic order. Healthy butterflies and adult parasitoids were released back at the site whenever possible.

Many volunteers collected rainfall data at the site on at least a weekly basis. They also recorded the temperatures in full sun and shade when they monitored.

Data collection, management, and analysis

For the first 5 years of the project, volunteers returned data on paper forms or a spreadsheet template. We checked entered data against hard copies for validation and contacted volunteers when values seemed unusual. Data were managed in a Microsoft Access relational database. In 2002, volunteers used a web-based data entry format.

The presentation of phenological patterns in oviposition utilizes data from sites in the Upper Midwest, Northeast, and southern United States. We focused our statistical analyses of temporal and geographic variations in monarch abundance on the egg stage, since the lack of mobility of eggs makes this the best representation of monarch reproduction. We limited statistical analyses to sites in the Upper Midwest and Northeast regions because these regions comprise the vast majority of the available data. The Upper Midwest includes all sites in Minnesota, Wisconsin, Michigan, and Iowa. The Northeast includes U.S. sites east of the Great Lakes and north of the 40° latitude, as well as eastern Ontario and Quebec. Most analyses exclude agricultural fields and gardens. To analyze egg abundance, we used a generalized linear model developed in SAS with a binomial distribution and a logit link function (Agresti 2000; K. Barnes, pers. comm.). The response variable was the number of eggs observed per milkweed examined for the 1053 monitoring events that fit the criteria just described. Fixed-effects predictors included year, region (Upper Midwest or Northeast), latitude, and first, second, and third order year-by-week interactions to model the nonlinear peaks and valleys in oviposition. Site was included as a random effect. We included a repeated-measures component in the model to account for the fact that sites were monitored 1 to 20 times during each year. This analysis included data from only 1997 to 2000.

As an estimate of monarch survival, we used the ratio of the total number of fifth instars to the total number of eggs observed in each state, limiting the calculations to nonagricultural sites in the Upper Midwest and Northeast regions. Only sites with more than 10 monitoring events in a given year were included in this analysis.

RESULTS

Program results

An exact number of project participants is difficult to obtain, since many volunteers participated with their families or students. To date, over 300 volunteers have participated in the program. These participants include secondary and college students, teachers, naturalists, scientists, retirees, and people from other professions and backgrounds. Together, they have monitored a total of 264 sites during the first 6 years of the project, with 54 sites that have been monitored for 2 or more years. Each year, 29% to 67% of participants continue monitoring the following year.

Approximately 36% of sites were monitored by informal or formal educators who incorporated the project into learning activities. Teachers and students were excited to be participating in this “real science” endeavor. For example, Jane Borland, a high school teacher in Texas, has monitored with students since 1998. In 2000, she wrote:

> [We are] about to begin our third year of monarch larval monitoring. The first year, two students participated. As the Texas summer heat brought temperatures over 38°C each day, it became mandatory to monitor early in the morning, much to the dismay of sleepy teenagers. However, they were so interested in doing real scientific research that they made little fuss. To make things more challenging, we did not find a single egg or larva during the summer months. Each week, I reinforced the point that having data that showed no summer activity would one day be important to us. As fall migration season and cooler temperatures arrived, our enthusiasm was revitalized as we began to find eggs and larvae. There are currently eight dedicated students on our core research team. Once the students find their first eggs or larvae, they are hooked. . . . They are proud of their work and the fact that they are conducting valid scientific research. (J. Borland, pers. comm.)

Almost 90% of the data met the criteria for inclusion in the monarch abundance database by having at least one monitoring event in which the date, number of milkweeds examined, and number of monarch eggs and larvae observed were all clearly indicated. An additional 4% of sites returned only data on parasitism rates, and some participants returned data that lacked sufficient quantification for inclusion in either database. Table 2.1 summarizes the monitoring efforts, including only sites with data on monarch abundance. The sites are in 29 states and 2 Canadian provinces (figure 2.1), with most sites in the Upper Midwest.

Table 2.1. Summary of monitoring effort

Year	No. of sites	Average no. of weeks monitored (range)	Average no. of ramets examined/ week/site (range)	Upper Midwest	Northeast	Other locations
1997	18	10 (1–25)	184 (9–718)	61%	22%	17%
1998	17	10 (2–20)	122 (28–305)	76%	12%	12%
1999	35	11 (1–22)	96 (5–344)	60%	14%	26%
2000	41	12 (1–30)	122 (10–437)	59%	20%	21%
2001	21	11 (1–21)	127 (9–282)	76%	5%	19%
2002	69	9 (1–31)	74 (5–267)	41%	13%	46%

Note: All sites with data from at least 1 monitoring event are included. “Upper Midwest” includes sites in Minnesota, Wisconsin, Iowa, and Michigan. “Northeast” includes sites in Maine, New Hampshire, Vermont, Quebec, eastern Ontario, New York, Rhode Island, and Pennsylvania. Sites monitored as part of the USDA-funded research are not included.

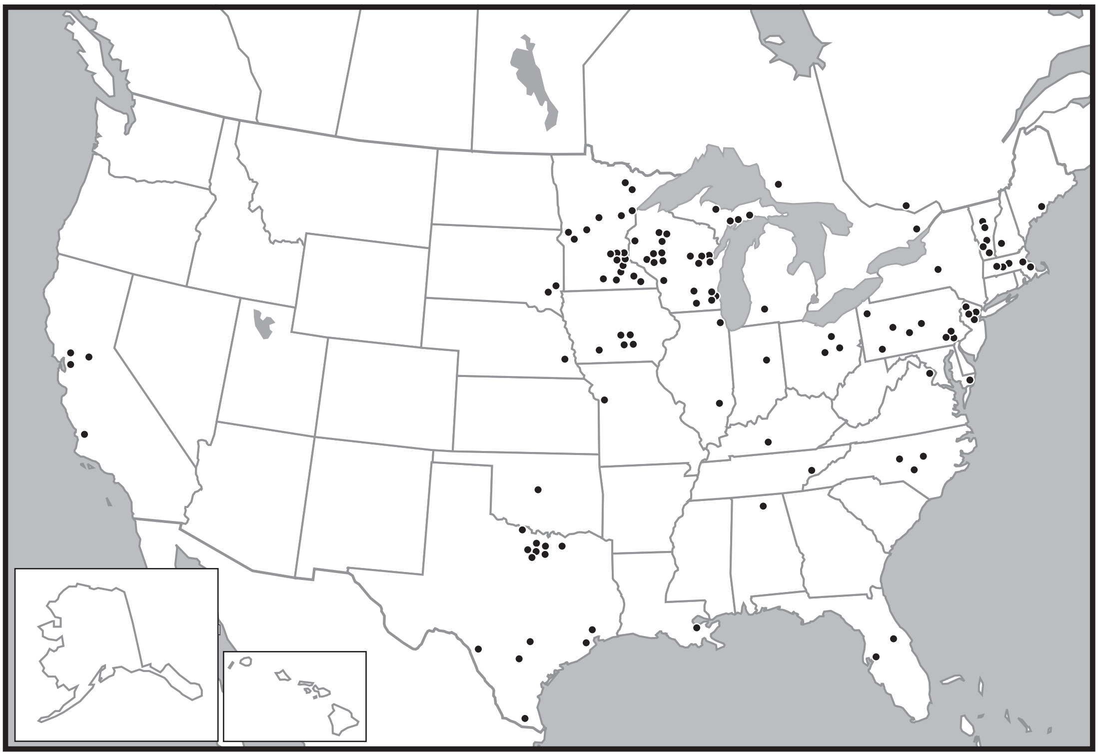

Figure 2.1. Location of sites for which we have data for at least 1 year.

Phenology and intra-annual patterns

Most observers in the Upper Midwest and Northeast monitored *Asclepias syriaca* (common milkweed). Observers in the southern United States monitored a wide variety of native species and the introduced *A. curassavica* (tropical milkweed).

Figure 2.2 shows egg densities over time for the Upper Midwest. Only data from 1997, 1998, 2000, and 2002 are illustrated to make the figure clearer; 1999 and 2001 values were quite similar to those in 2000. There tend to be two distinct peaks in egg densities, although the timing of the peaks varies among years. The first peak was earliest in 1998 and latest in 1997. The timing of the second peak in egg density is more consistent, occurring during the last half of July in all 4 years. This peak is wider than the first and probably represents overlapping generations (Borkin 1982). The end of breeding is more consistent across years; few eggs were observed after mid-August.

Figure 2.3 shows egg densities in Northeast sites. Only data from 2000 and 2002 are shown, as those are the only years in which more than two northeastern sites were monitored for most of the breeding season. There was not a clear pattern of peaks in egg abundance in 2000, and there was a much later first peak in 2002. Eggs were observed later in the season in the Northeast than in the Upper Midwest during both years.

Figure 2.4 illustrates monarch densities for representative sites in the southern part of the monarchs' breeding range in 2000. As expected, monarchs were observed earliest in Texas (figure 2.4a) and about 3 weeks later in southern Illinois (figure 2.4b). Both sites had few monarchs in midsummer but showed a late-summer or early-fall peak in abundance. The amount of fall breeding activity is especially striking

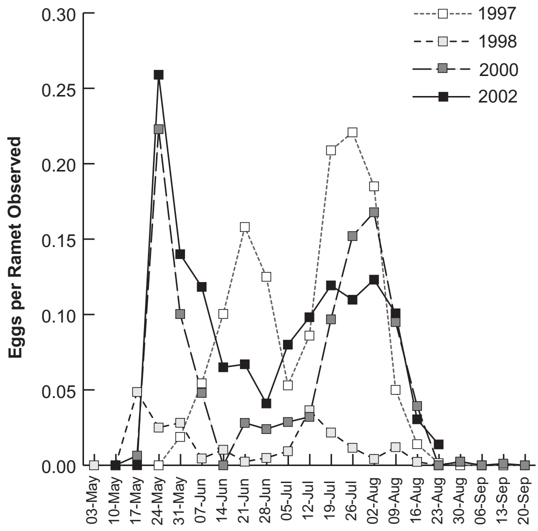

Figure 2.2. The number of eggs per milkweed observed over time in 4 years in the Upper Midwest. Points represent all of the eggs observed throughout the region in a given week divided by all of the plants observed. The x-axis shows the first day of the week during which sites were monitored.

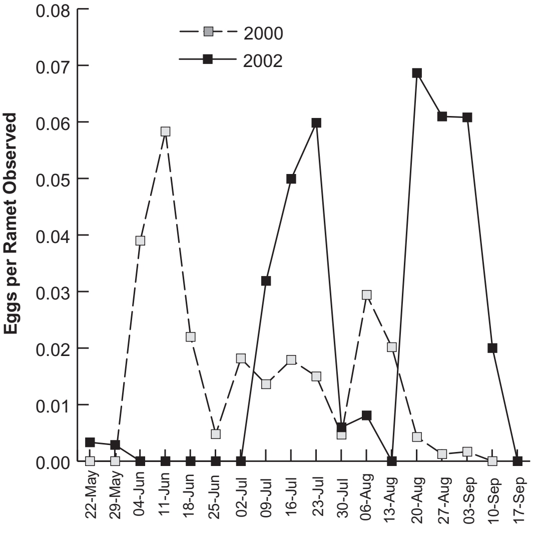

Figure 2.3. The number of eggs per milkweed observed in 2000 and 2002 in the Northeast. Points represent all of the eggs observed in the region in a given week divided by all of the plants observed. The x-axis shows the first day of the week during which sites were monitored.

for gardens planted with *A. curassavica*. For example, Borland found 678 monarch eggs over 5 weeks in a Texas garden with 130 *A. curassavica* plants (figure 2.4c).

Table 2.2. Egg density analysis: coefficients for region, latitude, and year

Effect	Coefficient	Standard error	*p* value
Region (Northeast)	–1.25	0.40	0.0017
Latitude	–0.09	0.10	0.3846
Year 1997	9.0741	5.0928	0.0751
Year 1998	3.4211	4.7499	0.4716
Year 1999	6.4826	4.6771	0.1661
Year 2000	6.5122	4.5994	0.1572

Note: The regression model included year, region, and latitude as fixed-effects predictors and site as a random effect. Repeated measures over weeks within a site were also included. The model included year*week, year*week^2, and year*week^3 to model the nonlinear relationship between egg densities and week. Year-by-week interactions and site all contributed significantly to the model.

Table 2.3. Egg density analysis: results of contrasts between years 1997 to 2000

Contrast	*df* (no./density)	F value	*p* value
1997 vs. 1998	1/968	4.28	0.0388
1997 vs. 1999	1/968	1.00	0.3175
1997 vs. 2000	1/968	1.06	0.3033
1998 vs. 1999	1/968	3.00	0.0834
1998 vs. 2000	1/968	3.64	0.0569
1999 vs. 2000	1/968	<0.00	0.9831

Note: There were significant contrasts among the years, with the probability of a milkweed plant having an egg significantly lower in 1998 than in any other year.

Temporal and geographic variation in egg densities

Tables 2.2 and 2.3 show the results of the regression analysis of the relationship between egg densities and temporal and geographic factors. Region had a significant effect, with per plant densities higher in the Upper Midwest than in the Northeast (figure 2.5). Egg density did not increase or decrease with increasing latitude (see table 2.2). There were significant contrasts among years, with egg densities significantly lower in 1998 than in other years ($p < 0.1$, see table 2.3).

Monarch survival

Figure 2.6 shows survival estimates in the upper midwestern sites. There are not strong differences in ratios among years, with means ranging from about 10% to 20%. These values are well within the range of survival observed in more controlled studies (Borkin 1982; Zalucki and Kitching 1982; Oberhauser et al. 2001).

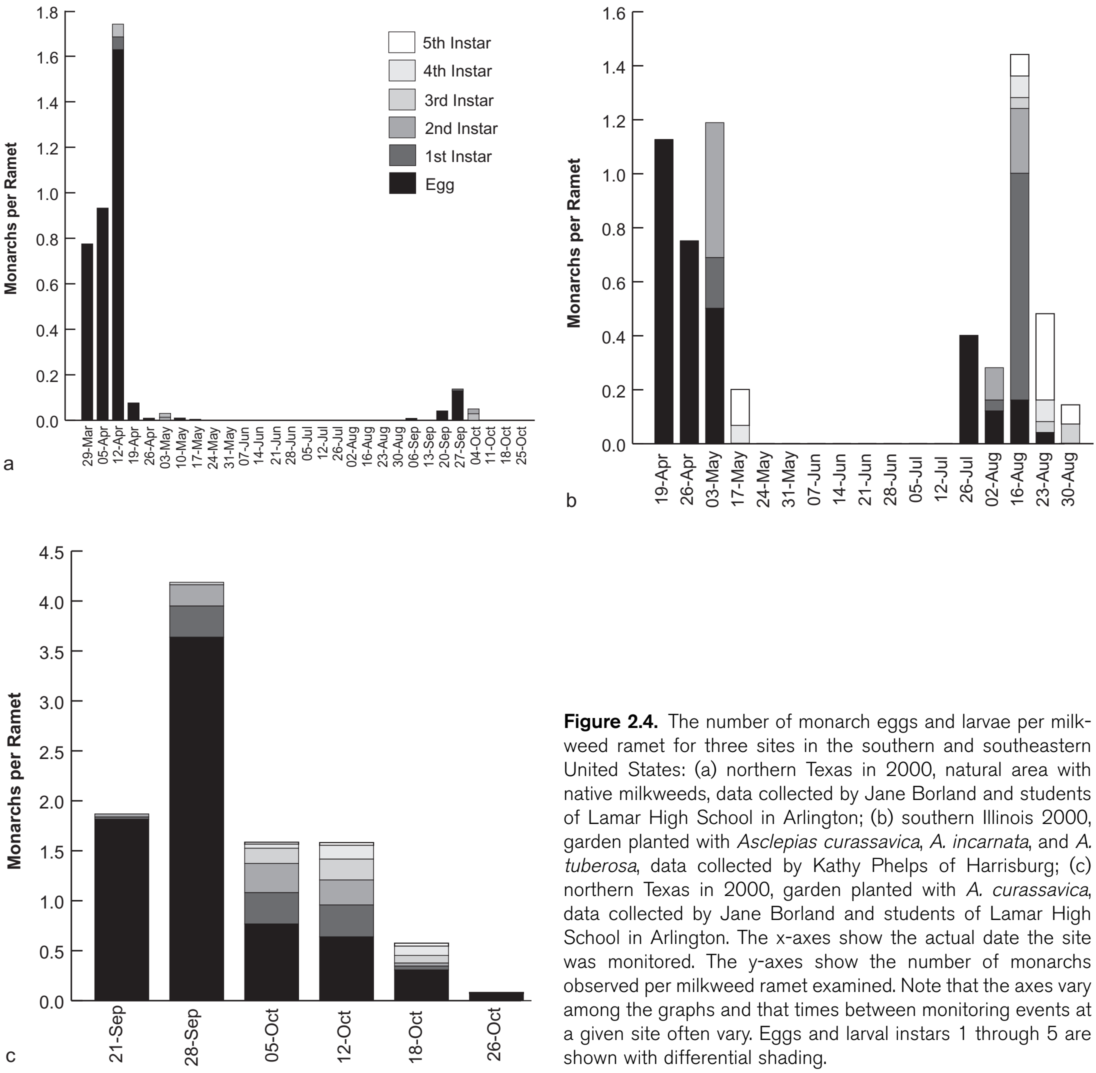

Figure 2.4. The number of monarch eggs and larvae per milkweed ramet for three sites in the southern and southeastern United States: (a) northern Texas in 2000, natural area with native milkweeds, data collected by Jane Borland and students of Lamar High School in Arlington; (b) southern Illinois 2000, garden planted with *Asclepias curassavica*, *A. incarnata*, and *A. tuberosa*, data collected by Kathy Phelps of Harrisburg; (c) northern Texas in 2000, garden planted with *A. curassavica*, data collected by Jane Borland and students of Lamar High School in Arlington. The x-axes show the actual date the site was monitored. The y-axes show the number of monarchs observed per milkweed ramet examined. Note that the axes vary among the graphs and that times between monitoring events at a given site often vary. Eggs and larval instars 1 through 5 are shown with differential shading.

DISCUSSION

Data validity

Data validity is an important issue for citizen science projects because of high observer variability, inconsistencies in observations, and other peculiarities of the method. Unfortunately, the structure of our study does not allow us to quantify the accuracy of volunteer-collected data. We have no way of knowing how the data ought to look because there have been no other studies in which monarch densities were measured over large spatial and temporal scales. We can, however, look at factors that might indicate how valid the data are.

Our first concern was the volunteers' ability to find monarch eggs and larvae. We know from our own monitoring that the total number of eggs per milkweed rarely exceeds 1, at least for the large, nonagricultural sites in the Upper Midwest. Nearly all volunteer observations were lower than 1 egg/milkweed. In addition, the phenological patterns in oviposition evident from the volunteer data are similar to those we have observed ourselves. If volunteers were greatly overestimating egg densities, perhaps by mistaking milkweed latex as monarch eggs, we would expect more observations exceeding 1 egg/milkweed and records of monarch eggs continuing into late August. Evaluating whether volun-

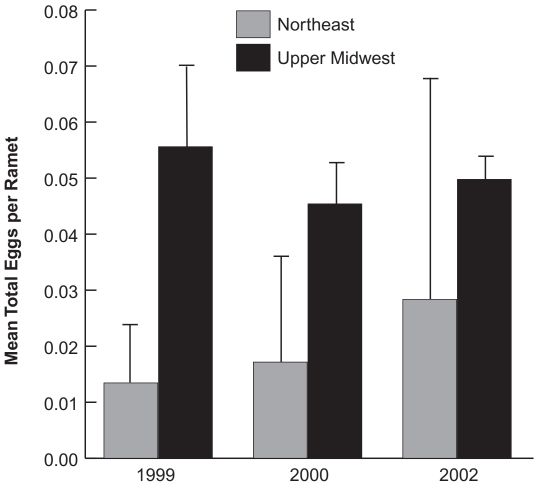

Figure 2.5. Mean total number of eggs observed per milkweed examined in 1999, 2000, and 2002, averaged across states in the Upper Midwest (Minnesota, Wisconsin, Michigan, and Iowa) and Northeast (1999—Vermont, Pennsylvania, and Quebec; 2000—New Hampshire, Vermont, New York, Pennsylvania, and southeastern Ontario; 2002—Vermont and Pennsylvania). Error bars show standard deviations.

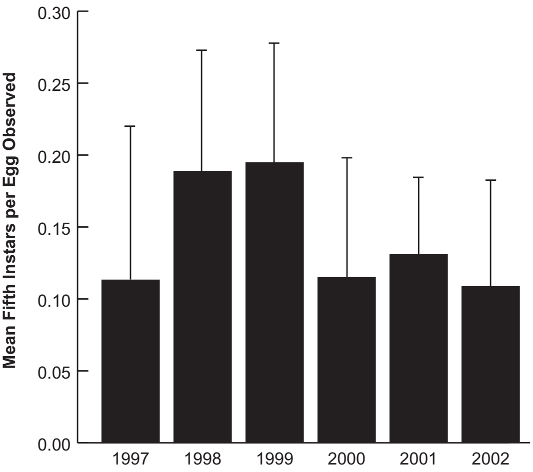

Figure 2.6. Mean ratios of fifth instars to eggs for upper midwestern sites, calculated by averaging state means within each year (state means are calculated by dividing the number of all of the eggs observed in the state in a given year by the number of all of the fifth instars observed in that year). Error bars show standard deviations.

teers are underestimating egg densities is more difficult. From our experience in training volunteers and watching them in the field, it seems that the less experience a volunteer has, the more careful he or she is when examining the milkweeds. In addition, the rough calculations of ratios of fifth instars to eggs suggest that volunteers locate most eggs. However, there were clearly exceptions, such as a few volunteers who reported more fifth instars than eggs. Our anecdotal observations suggest that volunteers are at least as accurate as the field assistants that we have hired to collect similar data. In fact, one of the data sets from our cooperating scientists' study (Oberhauser et al. 2001) had to be analyzed separately when we discovered that some of the field assistants did not distinguish first and second instar larvae correctly.

The dull color, small size, and cryptic behavior of first instars make this the most difficult stage to locate. In the absence of data on misidentification of larval instars, our analyses to date considered only fifth instars because the distinct characteristics of this stage make it the least likely to be overlooked or misidentified. Volunteers might overestimate the fifth instar densities because they can be seen from several meters away; volunteers observing a fifth instar from afar may be more likely to include that milkweed in their sampling. The fifth instar–egg ratios indicated that this is not a problem for most volunteers (see figure 2.6).

Phenological patterns

With three generations of monarchs predicted in the Upper Midwest (Borkin 1982; Zalucki 1982), one might expect to see three peaks in egg densities. However, differences in development time between the first and later generations result in just two peaks. The first generation, offspring of butterflies that were larvae in the southern United States earlier in the spring, can take up to 8 weeks to become adults owing to cool spring temperatures (Malcolm et al. 1987; Cockrell et al. 1993). The earlier spring migrants arrive, the longer the development time of the first northern generation (Cockrell et al. 1993). Thus, the time between the two peaks in egg densities varied from 5 weeks in 1997 (when monarchs arrived in the Upper Midwest later than average) to 8 weeks in 1998 (when monarchs arrived in the Upper Midwest earlier than average) (see figure 2.2). The second peak in egg densities represents the second and third northern generations of butterflies. These generations have a shorter development time, owing to warmer temperatures. Therefore, the eggs at the beginning of the second oviposition peak develop into mature adults that lay the eggs at the end of the peak.

The existence of several narrower peaks in the Northeast in 2000 (see figure 2.3) may be due to the fact that Northeast sites were located in two subregions, the Vermont/New Hampshire area and southern Ontario. The timing of monarch reproduction may be somewhat different in these two areas, leading to the appearance of several peaks when data from both areas are combined. In 2002, when there are clearer peaks, the only sites that had reported data at the time of analysis were in Vermont and Pennsylvania. Additional data will help to clarify this pattern.

Urquhart (1987) observed fall monarch reproduction in the southern United States, but there has been little research to describe its extent. Calvert (1999) suggests that some monarchs emerging in the fall disperse southward while laying eggs, similar to the northward spring migration. Observations of our volunteers in the southern states further quantify the amount and extent of this reproduction. Monarchs appear to achieve at least one additional generation in the South in late August and September.

Interannual variation in monarch abundance

Data on year-to-year differences in egg abundance allow us to look for relationships between egg and adult densities at different times of the year. Since our sample sizes are larger during the second peak in abundance (see figure 2.2), our discussion focuses on this peak and not the more variable and less reliable first peak. Reports to the Monarch Watch listserv related low numbers of migrating monarchs in 1998 (Taylor 1999), matching the egg densities that we observed that year. Comparisons with overwintering monarch populations are less clear. The colonies appear to have been several times larger in 1996–1997 than in subsequent years (García-Serrano et al., this volume), correlating with our high 1997 egg densities (see figure 2.2). Interestingly, breeding seasons for which high egg densities are evident in the MLMP data (such as 1997) are not consistently followed by large overwintering colonies; 1997–1998 was a relatively low-abundance year in the overwintering colonies (García-Serrano et al., this volume). This lack of correlation may be due to variations in adult survival rates during the migration or overwintering periods, and suggests that conditions faced during the overwintering or migration stages of the monarch's annual cycle may drive population dynamics more than conditions during the breeding stage. The year following a catastrophic storm in the overwintering colonies (2002; see Brower et al., this volume) has the second-lowest second peak (see figure 2.2), supporting this chain of cause and effect.

Monarchs arrived in the Upper Midwest earliest in 1998, the year that also had the lowest abundance. These two statistics may be unrelated, or they could reflect a biological relationship. Perhaps the slow development that results from early arrival and cool temperatures means that monarchs are exposed to more predation. Factors that resulted in earlier movement from the southern regions could also cause lower abundance.

Geographic variation in monarch abundances

Regional differences in egg densities support previous observations (Malcolm et al. 1993; Swengel 1995), with lower densities in the Northeast than the Upper Midwest. There are several possible explanations for this pattern. Malcolm and coauthors (1993) suggested that fewer monarchs migrate to the Northeast because of the barrier of the Appalachian Mountains. They found that the majority of adult monarchs captured in Pennsylvania and Massachusetts had fed on *A. humistrata* as larvae, a milkweed species restricted to the southeastern United States. This pattern suggests that the monarchs whose offspring colonize the northeastern region are a relatively small subset of the entire population that fly east from Texas and then lay eggs in the Southeast.

Biotic factors may also drive these patterns. Although the most common milkweed species in both regions is *A. syriaca*, the distribution and abundance of the host plant probably differ. For example, the overall area available for breeding may be larger in the Upper Midwest. A large portion of the Upper Midwest is farmland; Oberhauser and colleagues (2001) demonstrated that agricultural habitats are important contributors to the total monarch population in that region. More nonurban habitat in the Northeast is forest and contains less milkweed. Finally, the lower abundance of monarchs in the Northeast may be due to abiotic factors such as temperature, humidity, and cloud cover.

Monarch survival

Our estimates of monarch survival indicate that 10% to 20% of monarch eggs live to the fifth instar stage. Causes of mortality in eggs and early instar larvae may include predation, host plant defenses, and abiotic factors such as lethally high temperatures. We plan to use temperature records to develop models to estimate monarch survival more precisely, and utilize volunteers' observations of potential predators and milkweed condition to help identify causes of mortality.

CONCLUSIONS AND FUTURE OBJECTIVES

The MLMP has established a standardized methodology for monitoring monarch populations that can be used successfully by volunteers in a variety of habitats. We have organized a network of volunteers to monitor several regions of the United States and Canada, collecting data that document temporal and geographic differences in monarch abundance. Other aspects of the data—including female choice of oviposition plants and habitats, effects of landscape features, and sources of mortality—remain to be explored. The project will eventually provide a long-term data set that will allow continued contributions to our understanding of monarch distribution and abundance.

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