CHAPTER 3

North by Northeast

LESS THAN A WEEK AFTER WE HAD RETURNED HOME from our trip to the Monarch sanctuaries at El Rosario and Sierra Chincua, a severe winter storm hit the Michoacan mountains. Winds estimated at over 100 km/h (62 mph) drove snow and ice through the mountains, downing many trees and damaging most of the others that remained standing. Two small colonies of Monarchs at La Herrada and Cerro Pelon were decimated and the mortality rates for the relatively small numbers of butterflies there were estimated at upwards of 80 percent.

The storm was not considered to be as strong near the town of Angangueo, the base for our—and many other—expeditions to the El Rosario and Sierra Chincua colonies. Still, the Chincua colony received more than a meter of snow (over 40 in.) and had low temperatures of –8°C (18°F). El Rosario fared marginally better, with only about a tenth of the snow (nearly 10 cm or 4 in.) and temperatures only slightly below freezing (–4°C or 25°F). Mortality at the two colonies was estimated at nearly eight percent but because these are two of the most populous colonies—especially Sierra Chincua that year—the number of butterflies lost was almost as high as that at La Herrada and Cerro Pelon.

So to put this all into perspective, we visited the colonies during a year that is widely thought to have had one of the lowest roost recruitments since attempts have been made to estimate the numbers of butterflies at the colonies. And shortly after we left, a storm further reduced the population to a still lower number. Of course, this number was still in the 18 to 22 million range but this is considerably less than the beginning number from this or previous seasons. What effect would the low number of migrants have on the journey north that year? What effect would it have on the breeding population, and subsequent southward migration?

Amazingly, the low population size of northward migrants had little effect on the timing of their reappearance at their first stops in northern Mexico and Texas.

Guided by the sun, increasing day length and the slow, inevitable change of season, female Monarchs on the migration north arrive in Texas. The first stop on their northward journey and one of their last on the migration south, Texas is the funnel through which the entire population of migrating Monarchs must pass.

At the Stengl "Lost Pines" Biology Station near Smithville in central Texas, we generally expect to see our first Monarchs within a day or two of March 18, and March 2001 was no exception—a female was seen in the yard on March 19. By the time that Monarchs get to central Texas the population has dispersed sufficiently to make it difficult to estimate numbers, but my impression that year was that the numbers did not seem unusually small.

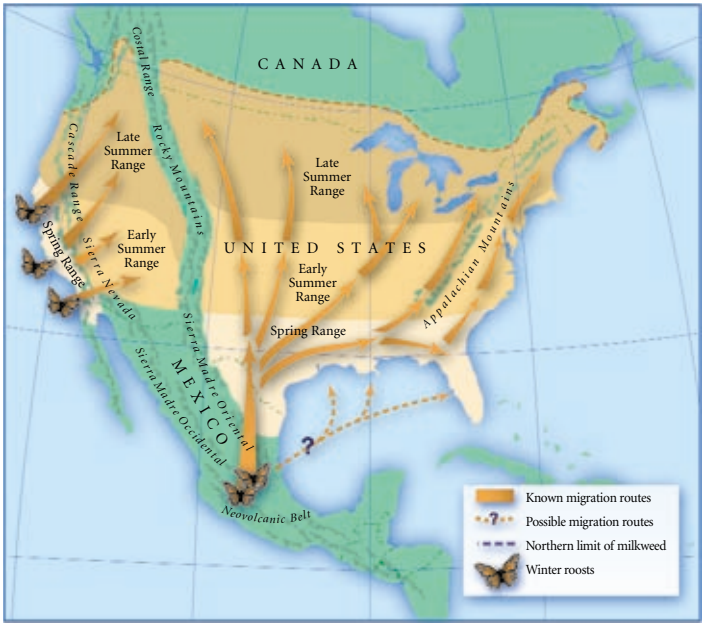
The first arrivals in Texas in mid-March are "primary" migrants; isolated individual butterflies that have mated at the overwintering colony (or shortly thereafter) and traveled as far north as the station. Along the way, females seek out seedlings and young milkweeds, lay an egg or two, and continue north, leaving a generation of progeny behind them to continue the journey north. Think of it as a "leap-frog" migration with the generation left behind eventually surpassing the parents in their northward trek. We don't usually see these "secondary" migrants at the "Lost Pines" until mid-April when there's a noticeable influx of bright orange, fresh adults.

We also often don't see any males until this second "wave" reaches us but sometimes we do see a number of first wave males. On March 18, 2002, for example, I watched a group of eight or so Monarchs nectaring at pear blossoms. These were just about the only thing in bloom because we had had a number of late season freezes that delayed most of the spring wildflowers. At least three of the butterflies at the tree were amorous, frustrated males that were aggressively attacking the others, knocking them out of the air and attempting to copulate on the ground.

We're lucky here in central Texas if we see Monarchs for more than about a month in the spring and the same in the fall. Not at all like what I was familiar with in southern Ontario, where they would generally arrive in late May and we could see Monarchs just about everywhere until late September or so. Still, Texas is like a funnel through which the entire population of migrating Monarchs must pass, being one of their last stops on the migration south and one of their first on the journey north…

The First Stop

It's difficult to underestimate the importance of Texas in the migration of the Monarch butterfly, regardless of whether you are considering the flight north in the Spring or the migration south in the Fall. Texas is the first stop north and



Each spring, millions of Monarchs depart their overwintering roosts in Mexico, embarking on a long journey north. Following the gradual availability of milkweeds as spring advances from south to north, the Monarchs migrate in leap-frog fashion, with each successive generation eventually surpassing the parents in their northward trek.

the last stop south. What effect do conditions in Texas have on the population of females that are flying north in the spring?

Guided by the sun, increasing day length and the slow, inevitable change of season, females painstakingly seek out suitable milkweeds on which to lay their eggs. The problem is that at this time of year these are plants that are in many cases barely out of the ground. I've tried to find milkweed seedlings and sprouts as late as mid-April in central Texas and can readily attest to the painstaking part. Luckily, the butterflies are much better at this task. It's fascinating to watch a female Monarch cruising low over the meadows and fields, alighting every now and then to test the foliage of some potential sprout or another.

The availability of host plant sprouts at this time of year assumes that it has been a "good" year. If there has been sufficient winter rainfall, if the winter hasn't been cold, with long, hard freezes, and there have been few (if any) late season freezes—and if the milkweeds had the time, rainfall and nutrient resources in the previous growing season to complete their growth or set seed—

The first Monarch arrivals in central Texas in mid-March are "primary" migrants, butterflies that have lived for as much as eight months, have mated at the overwintering sites, and flown a further 1,200 km (750 mi) north. A month later, a second generation of butterflies arrive, from the eggs the females laid along the way.

MILKWEEDS AND MIGRATION

As we have seen, the Danainae butterflies, of which the Monarch is a member, are primarily tropical and subtropical in origin. Not too surprisingly, the plant family Asclepiadaceae—including the milkweed host plants of the Monarch, members of the genus *Asclepias*—are similarly tropical and subtropical in origin. Concordance in the worldwide distribution of these two groups is expected and, of course, the Monarch wouldn't travel to and from higher latitudes if there were not temperate members of the Asclepiads. So the question "Why does the eastern North American Monarch migrate from lower to higher latitudes, then return each winter?" could easily be reconsidered as "Why are there temperate members of the milkweed family?"

The milkweed family is much larger and far more extensive than the number of butterfly taxa that use it as host plants. There are nearly 350 genera containing some 3,000 species of these herbs, shrubs, twining lianas and (rarely) trees, around the tropics. The large number of species and genera is a good indication that the Asclepiadaceae is a very successful plant family within suitable habitat. If we examine the temperate species, we find that less than 5 percent of the family is found outside of the tropics. In other words, Asclepiads had no need to colonize temperate regions to be successful. So, why bother? Well, because they can—there's more than a little truth to the old adage that "nature abhors a vacuum."

The fact that milkweeds occur outside of the tropics, together with the fact that they are seasonal and require fairly specific conditions in which to grow (because they have adapted from tropical ancestors) and the Danaine's predilection for migration go a long way to explaining the reach of Monarch migration and continental recoloniza-

then there will be milkweed sprouts for females to find and lay eggs on. But if any of these conditions haven't been met, or if the butterflies leave the roosts earlier than they should, then they could arrive before there are plants available for their eggs. This is exactly what may have happened in Texas in 1995 and 1996, then again in 1998 and 2000.

Droughts can have drastic effects on plant survival and their availability, not just on suitable milkweed host plants, but on the flowers and nutrient sources that are needed to sustain Monarch flight and life as well. Even if there are barely adequate nectar resources, droughts reduce the growth of milkweeds so that there are fewer leaves and smaller plants that may not be able to support the complete development of caterpillars. Leaf quality of drought-stressed plants also declines so those caterpillars grow more slowly and are more susceptible to disease and fungal pathogens, and to predation.

tion. In fact, if it weren't for a few wildly successful temperate milkweeds, it's very likely that the Monarch's phenomenal migration would be a great deal smaller and far less spectacular. Of the more than 100 species of Asclepias that occur in North America, only a half dozen or so are responsible for the extent of the northward expansion of the Monarch range that we know today.

The diversity of milkweeds declines as one moves north, from some 60 species in Mexico, to 30 species in Texas, a little more than 20 species in Kansas, around a dozen in Ohio and Southern Ontario, to only one or two around 50°N latitude and the states and provinces along the Atlantic seaboard. The "center" of Monarch summer breeding range—where more than 50 percent of Monarchs at the overwintering roosts originate from—is in the so-called "Corn Belt." At this latitude and position there are an average of around 14 milkweed species available for the Monarch.

Outside of the Corn Belt region the number of available milkweed species drops quickly to an average of less than five, with the most common species being *Asclepias speciosa*, *A. syriaca*, *A. incarnata*, and *A. tuberosa*. Early cardenolide "fingerprinting," which determined that Monarchs retained the chemical defenses of their host plants in direct correlation with that of the milkweeds that they fed on as caterpillars, showed that the vast majority of butterflies at the roosts—about 85 percent—had fed on *A. syriaca*, the common milkweed, or *A. speciosa*, the showy milkweed, species that only occur north of about 37°N latitude. Interestingly, Monarchs that feed on these two species, which are known to possess poor quality cardenolides, have the lowest concentration of cardenolides and are more likely to be preyed upon at the winter roosts.

Predators are legion, and Monarch eggs and growing caterpillars must contend with all manner of invertebrate and vertebrate predators anywhere in their range. But Texas also has a super-predator: fire ants. The imported alien fire ant, *Solenopsis invicta* (Hymenoptera), rather than the native *S. geminata*, is a major threat. Where this invasive species from South America is found the diversity of all terrestrial life, vertebrates as well as insects, spiders and other invertebrates, is greatly depressed.

You might be thinking, "aren't Monarch caterpillars protected by the noxious chemicals, the cardenolides, that they sequester from the milkweeds?" Unfortunately, as effective as these defenses can be against vertebrate predators, they seem to have little to no effect on many insect and spider predators. Fire ants are voracious predators of moth and butterfly caterpillars and controlled studies by Bill Calvert of Texas Monarch Watch have shown nearly 100 percent

Often despised as unattractive weeds with toxic leaves and sap, milkweeds (genus Asclepias*) are the Monarch's sole caterpillar food plants and are key to its survival and reproduction. The Monarch depends on only a small number of the more than 100 species of milkweeds found in North America. Shown, clockwise from top left: common milkweed (*Asclepias syriaca*), swamp milkweed (*A. incarnata*), showy milkweed (*A. speciosa*), and butterfly milkweed or butterflyweed (*A. tuberosa*).*

mortality of early stages wherever fire ants are present. Even where fire ant numbers are low (even the omnivorous fire ant is affected by drought conditions), Monarch egg and caterpillar survival is a long shot at best.

Still, in "average" years—although my friend and colleague, Larry Gilbert, a native Texan, is quick to point out that "average" in Texas is an anomaly—Monarchs do manage to replace themselves in enough numbers to continue their journey north by northeast. While the imported fire ant is thus far a southern problem, similar perils—weather conditions that modify plant growth, germination and reproduction or flowering, or cycling of predator populations in tandem with other factors—are encountered all along the journey north and throughout the eventual breeding range. Monarchs, like most other organisms, are at the mercy of the elements.

Continuity

Whichever way you look at it, Monarchs, like most other butterflies, face remarkable odds in their early stages, often approaching or exceeding 99 percent against them. Let's take a hypothetical case where a typical female Monarch is capable of producing and laying 500 eggs in her reproductive lifetime. This is reasonably close to the known lifetime fecundity of the 400 to 500 eggs that wild females with full life spans can lay. At a one percent survival rate, this would mean that only five of those eggs survive to become butterflies themselves. (In the real world, this is overly optimistic; in fact, many species of butterfly are lucky if they manage to have *one* of their progeny survive to replace them.)

A 5:1 replacement rate is actually pretty good. If half of 20 million northward migrating Monarchs are female, and half of those survive as far as Texas and even half of them have managed to lay all of the eggs that they are capable of laying then those 2.5 million females will generate 12.5 million progeny. This doesn't include the partially successful females that, say, average one replacement for every 100 eggs but don't survive long enough to complete their laying or those that have only been able to lay partial egg loads along the way to Texas because host plants are scarce. So it's not inconceivable that the 10 million females that began the journey could generate as many as 30 million progeny or so. Carry this through the next couple of generations and you can see that the next generation's 15 million females (one-half of 30 million progeny) may

BOOM AND BUST

Reliable estimates have established the Mexican Monarch population of fall 2001 around 120 million or so butterflies, four times higher than it was in fall 2000. This was a stark reversal of the declines in previous years; there were an estimated 110 million Monarchs in the fall of 1999 but only 30 million in the fall of 2000. In other words, instead of the possible 5:1 replacement rate seen in 2001 there was probably much less than a 1:1 replacement rate, possibly as low as 1:4 in 2000.

So what was different between the breeding seasons of 2000, when numbers declined drastically, and 2001, when the population size increased by some 500 percent? First and foremost, and potentially key, was the occurrence of a winter/spring drought in Texas that left Monarchs struggling to find enough flowers to maintain flight or host plants to lay eggs on before their conserved energy was depleted. (Remember, these are six- to eight-month-old butterflies that migrated all the way down to Mexico in the fall of 1999.) Worse, the drought in 2000 was not confined to Texas but was more widespread, throughout the southern portion of their normal breeding range.

This by itself would be enough to cause a significant decline in the first two generations, however, "good" conditions in the northern part of the breeding range could allow for a decent recovery that compensated for the loss due to southern droughts. In 2000, however, much of the northeast was plagued by cool, wet conditions that helped to prevent females from laying all of their eggs (if cool, wet weather prevents you from flying then you can't find plants on which to lay eggs). Eggs and early instar caterpillars may also have succumbed to fungus problems or pathogens while later caterpillar development would be slowed by the cool temperatures. The slower the caterpillar growth then the longer they are on the plants and available to caterpillar-hunting predators. Cool and wet can be just as damaging as hot and dry.

So, 2000 was a bust all the way around—drought affecting the returning migrants and the first generation in the south, and the opposite problem, wet and cool conditions, affecting the reproductive success of the second through fourth generations in the north. That year there were still caterpillars on milkweeds in late September and early October long after the migration south would have been well underway. But 2001 was a boom year with near to perfect conditions throughout the range. These two years, alone, provide a wonderful and useful illustration of the effects that environmental conditions during the northward recolonization phase can have on the size of the overwintering population in Mexico.

generate 45 million progeny, then 25 million or so females can yield 75 million butterflies, and so on. This scenario, given more than a little license in the variation between locations and generations, is possibly quite similar to what actually happened in 2001 (*See "Boom and Bust" above*).

A Monarch caterpillar feeds on a milkweed plant. To avoid the latex sap, which can gum up the mandibles of the caterpillar, Monarch caterpillars frequently "notch" the main veins of the leaves to stop the flow of latex through them. Like the Monarch, milkweeds are tropical in origin and only a relatively few species that have adapted to temperate conditions are responsible for the northward expansion of the Monarch's range, and their subsequent phenomenal migrations south.

A frenzy of Monarchs nectar at a Senecio near the overwintering roosts in Mexico. As Spring, and the journey to recolonize the continent approaches, the butterflies seek out nectar to fuel their flight north.

Journey's End

The end of the journey for a northward-migrating Monarch depends on which generation is undertaking the journey. The primary migrants do not, as a general rule, return much further north than Texas, although there are records of primary migrants presumed to have flown as far north as upstate New York. The majority of the secondary migrants from the generation that develops in northern Mexico and Texas will end their journey in the mid-eastern states or the southern Corn Belt states. In turn, the tertiary migrants from the second gener-

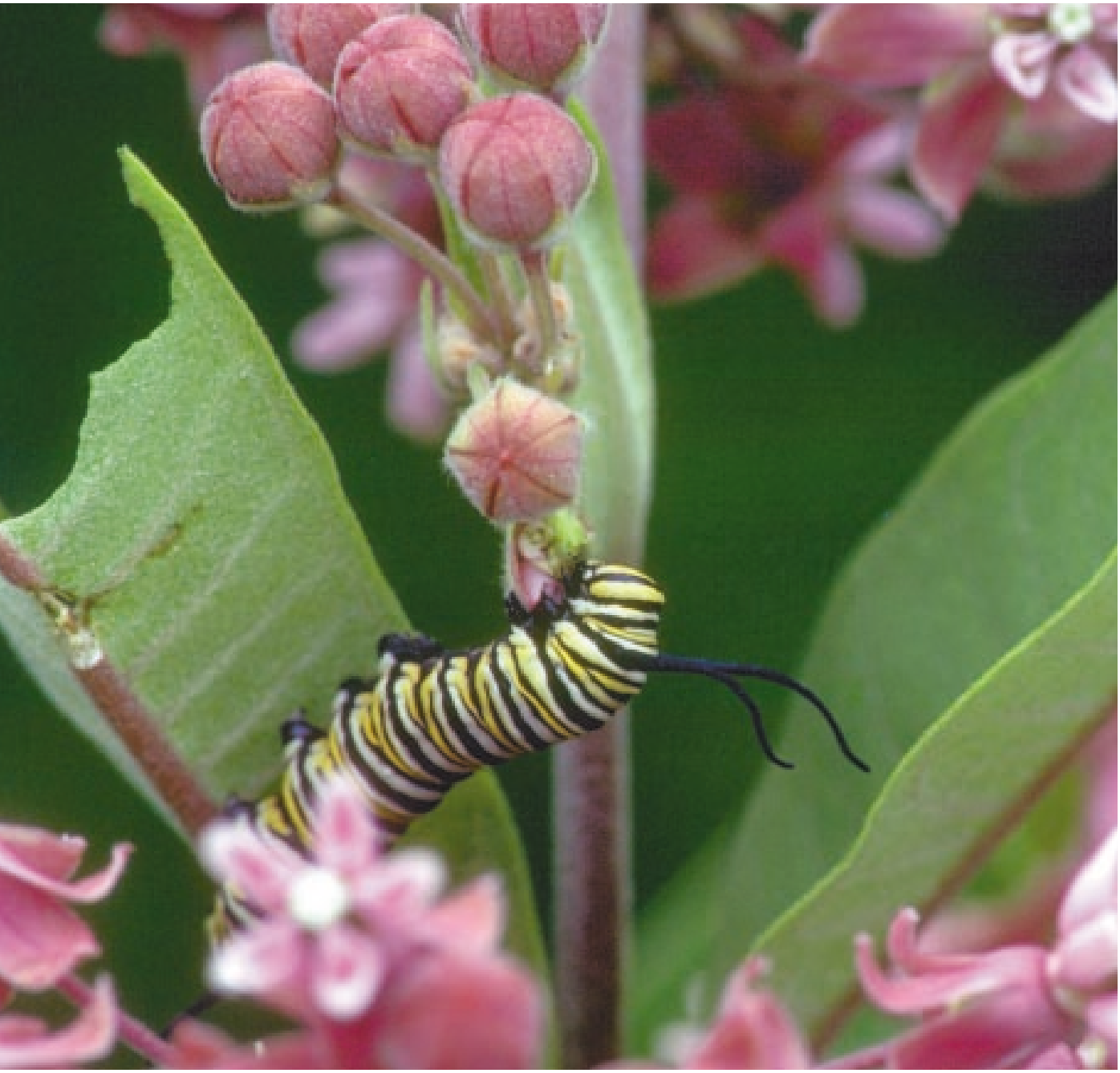
ation will journey further north and complete much of the recolonization of their range. This means that, depending on where you live in northeastern North America, you may not see Monarchs until as late as the end of May and beginning of June.

This is about the time that we were used to seeing our first Monarchs of the year in the Toronto area on the north shore of Lake Ontario. Monarchs really don't venture very far into Canada. Through most of the prairie provinces and western Ontario, the distribution of milkweed, and thus the distribution of breeding Monarchs, ends at around 50° to 52°N latitude, just a bit further north of the U.S.-Canada border at the 49th Parallel. Of course, central and southwestern Ontario is a different story since it reaches down to around 41°N latitude (Point Pelee, the southern tip of Ontario, is actually at the same latitude as the north border of the state of California).

The distributional limit of milkweeds and the potential breeding grounds of the Monarch in Ontario extend eastward from the line across the prairies up around the north and east shore of Lake Superior, along the northern shore of Lake Huron to Sudbury, North Bay and Highway 17 east to the Ottawa region. In eastern Canada, milkweed range limits include the southern and western parts of Nova Scotia, New Brunswick and the Gaspé region of the south shore of Quebec, crossing the St. Lawrence just northeast of Quebec City and continuing southwest towards Ottawa. Through much of this range there is only one or at most two species of milkweed, a far cry from the 30-some species that are known in Texas, or the nearly 60 species in Mexico. Ontario, with a total of 11 species, is the central portion of the Monarch's eastern range in Canada.

A northwest migrant refuels at flowers in south-central Texas. Droughts can have drastic effects not only on the availability of milkweed host plants but on the flowers and nutrient sources that are needed to sustain Monarch's flight.

Monarchs sometimes overshoot the range limits of milkweeds and there are records from as far north as the Hudson and James Bay lowlands, through the prairies up to about 56°N latitude, and even a record or two from the Northwest Territories north of Alberta and into northern British Columbia. Similarly, there



A Monarch caterpillar feeds on a milkweed plant. Like the Monarch, the milkweed is tropical in origin, although of the more than 100 species of milkweed that occur in North America, only a half dozen or so are responsible for the phenomenal migration of the Monarch and the northward expansion of its range.

*The end of the journey for spring migrants varies with the generation but some reach distances of more than 4,500 km (2,800 mi) from their winter roosts in Mexico. Here a male Monarch nectars at tansy (*Tanacetum vulgare, *Compositae) near North Bay, Ontario, a distance of 3,700 km (2,300 miles) north of Mexico."*

are almost yearly records of Monarchs being found in Newfoundland, although there are no native milkweeds on that island. Strictly speaking, Monarchs are not limited to the range limits of milkweed but they are not capable of reproducing beyond the limits of their obligate larval host plants.

So, depending on where you live in eastern North America, you may see primary returning migrants or the first, second or even third generation of Monarchs on their northward journey. And while people in Texas and the south might only see Monarchs during the two migration periods in the Spring and the Fall, folks in the north will see them pretty consistently for up to four months. During this time they will have two to three generations, each lasting for up to two months (about one month as egg, caterpillar and pupa, and up to one month as a butterfly), before the final generation once again turns its sights southward to Mexico.