Living in America

t was my first stark, bitter realization of our environmental carelessness. It had only been eight years since I last visited the northeastern corner of the Charles Sauriol Conservation Reserve in Toronto's East Don River Valley. I recalled this little valley—part of what is often called "a rare patch of urban wilderness"—as a wondrous butterfly-filled meadow, but it was now almost unrecognizable. What had once been a thriving, diverse ecosystem that sustained more than 35 or so species of butterflies was now choking, overflowing with an alien invader, the aptly named "dog-strangling vine" or black swallowwort, Vincetoxicum (Cynanchum) nigrum (Asclepiadaceae). That a place could change so much in so little time genuinely startled me.

My first visit to this spot was in the early summer of 1986. I had been systematically exploring the many access points into the Don Valley park system, doing some birding and butterflying before heading to work, when I "discovered" this little oasis, a meadow along the east bank of the East Don. It was alive with butterflies and I was intoxicated by the variety and abundance I stumbled into—I knew I was going to be late for work!

I remember watching Monarchs gliding among the milkweeds and seeing large numbers of at least a half-dozen species of hairstreaks, as many kinds of skippers, including the large silver-spotted skipper, both common and orange sulphurs and more tiger swallowtails than I think I had ever seen before, jockeying for positions on the blooms. I was thrilled to discover some turtleheads attended by Baltimore checkerspots along the bank of the river and pearly eyes along the edge of the woods. There were more kinds of wildflowers than I could count and every one seemed to have a butterfly, beetle or bee busily foraging on it.

This diversity—and my wonder at it—was one of those experiences that galvanized and reinforced my decision to return to school, to study the biology of plant and insect interactions, and devote the rest of my life to doing what I truly enjoyed.



Summer in North America seems idyllic for the Monarch, seen here in a field of goldenrods. Yet the Monarch's northern breeding grounds is no bed of roses, and is also home to a variety of predators, parasites and pathogens, from birds to vines, ants to humans, herbicides to genetically-engineered corn.

After having finished my undergraduate degree and more than halfway through my doctoral studies, I returned to this spot on a Toronto Entomologists' Association butterfly count in 1994. It was an eye-opener, to say the least.

The plant and butterfly diversity was less than half of what it had been eight years previously. Eight experienced counters encountered only seventeen species of butterflies with only single individuals of seven of those species—including only a single Monarch—being seen. Only a single individual of one of the half-dozen hairstreak species that I had marveled at in 1986 were still present and the milkweed they had been nectaring on had almost completely vanished under a carpet of swallowwort.

Appropriate to its name, the swallowwort had taken over and had nearly swallowed the entire meadow whole. The only region that still had some remnant of the previous diversity was along the very verges of the river. There, there were still some turtleheads with two or three Baltimores flitting amongst them but the pearly eyes along the boundary between the meadow and the woods had vanished, as had the sulphurs, the tiger swallowtails and most of the skippers.

In their places were hundreds of grass-feeding European skippers, Thymelicus lineola (Hesperiidae)—an invader that competes with the native skippers—tame bees, one or two species of beetles and the stark monoculture of the clonal swallow-wort. The destruction was almost total. If I hadn't already known this very mead-ow I would have doubted that there had ever been abundant life here. It reminded me uncannily of what purple loosestrife, Lythrum salicaria (Lythraceae), did to the marshes of the northeast (and is currently doing to much of the northwest)—move in, multiply and force everything else out.

It was not a pretty picture.

Trials and Tribulations

The main breeding grounds of the Monarch butterfly, that area north of about 38° or 39°N latitude up to the limits of milkweed range in Canada, is no bed of roses. My main thesis throughout this book has been that the conservation issues, problems, trials and tribulations that face the eastern North American Monarch population in their breeding grounds and along their migration routes are just as pervasive, just as endangering, and just as consequential as those that they face in their Mexican overwintering sites. What are these issues



Naïve birds, after tasting their first Monarch, seldom attack again. Here a Monarch nectaring at flowers shows the kind of damage to its left hindwing that results from a bird attack. A single "taste" of the noxious compounds in the wing scales that are left from caterpillar feeding on milkweeds is enough to deter most birds.

and how do they impact Monarch breeding, survival, migration and population dynamics? Is "living in America"—or perhaps more appropriately "dying in America"—an accurate description of the future of the Monarch butterfly in eastern North America?

Foremost among the issues facing the Monarch throughout its breeding range and migratory pathways—not unlike the overwintering sites—is habitat degradation, fragmentation and outright loss. Much of the breeding range and the areas traveled over during migration are the most populous parts of the continent. Surprisingly, habitat changes due to human land use modifications can at times be beneficial. For example, forest clearing for agricultural use in central Ontario between 1940 and 1990 produced a significant northward increase in the range of the common milkweed (*Asclepias syriaca*), from 43° to 47°N latitude, and a concomitant increase in the occurrence of the Monarch.

However, the majority of anthropogenic changes in land use and continuity have resulted in major losses of Monarch habitat. Other threats include the many environmental changes that accompany our "progress"; the myriad other forms of competition that occur between butterflies and humankind; changes to the natural balance of communities through the introduction of invasive, alien species; the wholesale spraying of pesticides and herbicides; and our failure to regulate, legislate or otherwise control our own activities.

Environmental Concerns

It is too early to know for sure, but global warming probably already impacts, or will soon impact, Monarch populations. We already know from research conducted on other species in both North America and Europe that butterfly ranges are expanding northward and contracting northward along their former southern edges. The ranges of entire species have been shown to have shifted up to 240 km (150 mi) north in a relatively short time (less than a century) and with a relatively small global temperature increase (estimated to be approximately 0.8°C or 1.5°F). The majority of climatologists and biogeographers predict that the rate of temperature change will likely double, up to 1.5°C (3°F), in less than one-half the time (within the next 50 years). Most agree that the consequences of this seemingly minor change to the distributions and population dynamics of plants and animals will be devastating.

What is most interesting when contemplating what global warming might mean to the Monarch is that the effects will almost certainly be negative at the overwintering roosts and potentially benign (or, in the long term negative) over the breeding range. The problem at the roosts is that the butterflies overwinter on mountain slopes, and mountains have finite heights—there is only so far you can move up a mountain slope before you reach the top and have nowhere else to go. Where will Monarchs roost if the mountains are not high enough to support the boreal community that might buffer the coming temperature change? There are already indications that the butterflies may be leaving the roost sites earlier than they once were, possibly a response to changes in seasonality already brought about by climatic warming.

At the other end of the range the consequences are less certain. It is probable that increasing temperatures will allow the current distributional limits of



milkweeds to shift northwards, while, at the same time, the southern limits will likely contract as conditions become less tenable. The net result of this shift could be neutral to the Monarch if agricultural land is cleared in the current northern forests at the same rate as the milkweed range moves northward, however, if there is a loss in available arable land the number of milkweeds and Monarchs could decline. Past changes in land use have generated an increase in range, likely with a similar increase in population size, but if this occurs again the larger potential population size may simply end up putting further pressure on the potentially reduced overwintering sites.

We have undoubtedly already seen harbingers of this last scenario in the past decade as a result of climatic changes triggered by El Niño and La Niña. These events, consequences of changes in the temperature of the Pacific Ocean Butterfly gardens are patches of urban habitat for Monarchs. While they must compete with human civilization for living space, and the few remaining patches of urban wilderness are dwindling, we can supplement those losses by providing needed habitat and resources for butterflies and other insects. due to sinking or rising cold or warm waters, have an untoward influence on upper air currents and the path of moisture-laden air borne on the westerly winds. Seemingly minor water temperature changes have generated major climatic shifts that alternately bring drought or cool, wet conditions to the south—having a drastic effect on Texas vegetation at critical times—or to the north. These events have already produced at least fivefold fluctuations in Monarch population size from year to year.

Monarch biologists are also interested in the effects that climatic variation and changes have on caterpillar growth and development, the length of flight seasons and the number of generations that occur at different locations, as well as their effects on adult butterfly lifespan, energetics, habitat choice, nectar and host plant resource availability, and reproductive success. We just don't know enough about these subjects to be able to accurately predict the outcome. What effect do unpredictable events such as storms and heavy rainfall have on population structure and dynamics? How do fluctuations in annual patterns of rainfall and sunshine affect host plant and nectar source availability and distribution? These are just some of the questions for which we do not have adequate answers. We still have a lot of work to do.

Competition with Us

Habitat fragmentation, degradation and loss are our fault. Very few organisms are able to change the environment that they live in. To be sure, there are beavers, elephants and a few others, but none of them has nearly as much of an impact on their surroundings as *Homo sapiens* does. Seemingly innocuous activities, pursuits that we take as normal, like traveling on highways, the new subdivision being built just down the block, the use and diversion of water for our kitchens, and reclamation of a bit of wetland here and there all add up to surprising consequences. One of my students once did a project on the cumulative effect of "minor zoning variance" petitions, which in a reasonably large metropolitan area individually amounted to no more than a few meters for every request, and the total loss of green space added up to at least a hundred hectares every year.

Highways are an interesting example of the staggering yet little realized effect that we have on wildlife. Anyone with more than a casual interest in but-terflies—or indeed any other kind of insect or animal—knows that vehicular traffic kills some individuals. We're used to seeing dead skunks or raccoons

along the side of the road. A recent study of the magnitude of the effect of such "road kills" on moths and butterflies along public roadways in the state of Illinois, however, opened a lot of eyes. The study revealed that the number of moths and butterflies killed along the 222,000 km (138,000 mi) of highways, toll roads, county, municipal and other roads in the state probably exceeded 20 million individuals per week. The cumulative mortality of Monarchs alone was estimated to be more than 500,000 individuals. This disturbing total is between one-fortieth and one-fiftieth of the entire population of butterflies that left the Mexican roosts in 2001 and 2002. Multiply this by the number of states and kilometers of roads that Monarchs have to cross, and this source of mortality alone may account for *millions* of deaths.

Over and above highways and the steadily increasing number of bigger and bigger vehicles that use them, we compete with nature on so many levels and in so many ways that it staggers the imagination. We build, expand, channel, convert and otherwise control nature to an incredible degree—now our actions are even changing climate and weather patterns. But these are the obvious ways that we compete with wildlife. It's the unthought, unremarked and unrealized that are so insidious but damage habitats in ways that we barely recognize while it's happening. It hasn't been that long since Rachel Carson's *Silent Spring* and I think that we have yet to prove that we've actually learned anything.

Consider the effect of introduced, invasive, alien organisms such as black swallowwort (*See "Swallowwort: An Alien Invader" on page 60*), and the restriction of Monarchs to milkweed hosts. The latter has been a cause of concern due to historical trends in weed control. For example, *Asclepias syriaca*, the common milkweed, is a very successful weed that grows well in a wide variety of agricultural and non-agricultural situations. For years, economic fears of reduced yields in field crops and misplaced fears of livestock being poisoned by the toxic chemistry of milkweeds have fueled many a noxious weed list and the wide propagation of weed control legislation that encouraged the wholesale destruction of plants wherever they occurred.

Of course, the fears of farmers and ranchers have little or no basis in fact: innovations in harvesting techniques over time have made potential yield issues inconsequential and I have yet to find an unequivocal case of livestock death from consumption of milkweeds. Anyone who has seen milkweed in pastures knows that livestock avoid the plants like the plague and that milkweeds are usually the tallest and most conspicuous plants in the entire field.

SWALLOWWORT: AN ALIEN INVADER

he black swallowwort or "dog-strangling" vine, Vincetoxicum (Cynanchum) nigrum (Asclepiadaceae), was intentionally imported from Europe and cultivated by the Canadian and United States governments during the Second World War as a potential source of latex, when the acquisition of rubber from the usual South American sources was interrupted by enemy activity along both coasts of North America. The war effort needed rubber for tires, gaskets, grommets and washers, rubber that was in short supply, so potential alternative sources ---including native species of Asclepias-were investigated. Needless to say, however, swallowwort escaped from cultivation and began to do what comes naturally to a vine: grow, reproduce, grow and reproduce some more.

The problem was black swallowwort was an invasive species, and in its new habitat it was able to grow and reproduce in the absence of all of the other species-herbivores, pathogens and competing plant species—that controlled the growth and size of the population in its native environment. We quickly learned that not only was black swallowwort (and native milkweeds for that matter) a poor, expensive source of latex for rubber production but it also grew rapidly, readily clambering up and over other plants-as vines are wont to doand successfully reproduced both sexually (seed produced from flowers) and asexually (new shoots generated via underground root expansion). In fact, it reproduces by underground runners so well that it quickly forms "monoclonal" (a large number of plants all with the same genetic makeup) stands

that choke, shade and kill competing plant species. Soon there's nothing left but swallowwort.

Particularly damaging for the Monarch is that black swallowwort is a member of the same plant family as milkweeds. It was feared that female Monarchs would mistake the plant for milkweeds and either lay enough eggs on the plant to reduce the number laid on their natural hosts or that the plant would prove to be incompatible with the normal development of their caterpillars. Two recent studies have allayed those fears somewhat, revealing that when given a choice between their usual milkweed and swallowwort (or, subsequently, no choice but swallowwort), females will overwhelmingly choose to lay on milkweed. The studies also confirmed that virtually none of the eggs that were laid on the swallowwort were able to complete development.

Potential problems with these studies, unfortunately, included that neither group controlled for the position of the plant in the test cages. For example, if the testing arenas were always set up so that the milkweed was always on the sunny side of the cage, is the plant or the direction of the sun responsible for the number of eggs on the plant? Similarly, neither group ever tested females only on swallowwort before they encountered a milkweed. In both studies, the researchers tested females on swallowwort alone only after exposing them to both the swallowwort and milkweed together for 48 hours. The question remains that if females are unable to find milkweeds would they accept swallowwort more readily? I actually doubt that this will make a difference to female host choice.



Intentionally imported from Europe during World War II as a potential source of latex, black swallowwort or "dog-strangling" vine, Vincetoxicum nigrum (Asclepiadaceae) quickly escaped from cultivation and has run riot in the wild, forming monoclonal stands that choke, shade and kill competing plant species including milkweeds. Yet being tall and conspicuous is not necessarily a virtue. Roadside and right-of-way mowing, most often for "beautification" but also sometimes for safety concerns, is another way in which we directly impact Monarchs, and other herbivorous insects and butterflies, without really thinking about it. The problem here, obviously, is the timing of mowing but it is also compounded by the simple fact that many roadside milkweeds tend to be tall, robust plants. Aesthetically they stick out like a sore thumb, often growing in relatively thick colonies of tall plants that may block sight lines and pose safety problems. Still, minimal maintenance regimes where only the very edges of the roads would be cut for safety reasons and timing mowing to coincide with natural interruptions of the developmental schedule of Monarchs would go a long way to reducing the impact of these practices.

Predators, Parasites and Pathogens

The variety of predators that target and consume butterflies is reasonably well known. Vertebrate predators include birds, lizards, snakes and a number of small rodents while invertebrate predators include spiders, dragonflies, ants, wasps and a number of predatory bugs and beetles. Unfortunately, surprisingly little is known about the specific predators of Monarchs. We do know that naïve birds, after tasting their first Monarch, will not attack one again, however, we also know that some birds at the overwintering roosts are habitual major predators of the resting butterflies. The Mexican birds bypass the noxious compounds in the butterflies by eating only those portions that have the lowest concentrations of the chemicals (which still kills the butterfly) or feeding *ad libidum* on Monarchs for a few days and then "purging" on other prey.

Lizards and snakes, while superb tropical and subtropical predators of a wide variety of butterflies and their caterpillars, are relatively scarce from the breeding range of the Monarch and are not likely to be a threat in North America. Rodents, particularly mice, shrews and voles, however, are another story. Has it occurred to you to wonder why Monarchs don't roost on the ground? After all, the ground retains daily heat better than the foliage of a tree. It's likely that the primary reason why Monarchs don't roost or rest on the ground is predation by rodents that could decimate an entire roost while the butterflies are too cold or otherwise unable to escape. Rodents are also major predators at the wintering grounds and of other roosting species of Danaines in the tropics.



One of the obstacles Monarchs face in North America is competition for their food. The Red Milkweed Beetle (Tetraopes tetraophthalmus, above) is one of several insect species that also feed on milkweed plants.

A large number and variety of invertebrate predators such as ants, wasps and beetles are likely to prey on the early stages of Monarchs. Here a second instar caterpillar is attacked by an assassin bug (Zelus sp., Reduviidae).



Relatively few invertebrate predators are capable of preying on large adult Monarch butterflies. Some of the larger dragonflies and many orb-weaving spiders will opportunistically consume them but others will ignore them or, in the case of some web-building spiders, cut them out of the web without eating them. It's also relatively common to find smaller insects, like assassin bugs, robber flies and others, with butterfly prey. Some of these insects and spiders may be sensitive to the cardenolides in the butterfly body while others may not (although the hunger state of the predator may have a great bearing on any decision to consume caught prey).

Vertebrate predators can and do feed on the immature stages (eggs, caterpillars and pupae) of butterflies, however, the large number and variety of potential invertebrate predators are far more likely to play significant roles in the early stage mortality of Monarchs. Ants, for example, will readily consume eggs and small caterpillars but will also attack, *en masse*, larger caterpillars and chrysalids. Even predacious mites and very small insects will devour eggs. Wasps and predatory beetles and bugs are very successful at killing caterpillars whenever they encounter them. The majority of these are opportunistic predators that kill and eat whatever they find but some, like the wasps and beetles known as "caterpillar hunters," intentionally seek out and target moth and butterfly caterpillars. However, on the whole, we know disappointingly little about specific invertebrate predators of Monarchs.

Of course, predation is not the only source of potential mortality in immature Monarchs. There are also a number of parasites and parasitoids (parasitoids are parasites that usually kill their host) that will attack any insect discovered. Some will only attack moths and butterflies while still others are specific to individual species or even life history stages of specific species. Many parasitoids are small insects (often flies or wasps) that target and lay their eggs in eggs, caterpillars or pupae of a host species. The growth and development of the immature parasitoids eventually kills the host.

One of the most important and best studied parasites of Monarchs is the Neogregarine protozoan parasite *Ophryocystis elektroscirrha*. This parasite infects dermal and reproductive tissues of Monarch and Queen butterflies and is transmitted via spores that drop off an infected female while she lays eggs or are laid along with an egg. When the egg hatches the young caterpillar ingests the spores on the leaf and egg surface and is thereafter infected with the parasite. Unlike a parasitoid, *O. elektroscirrha*, does not generally kill any stage

of the Monarch or interrupt reproduction of the butterflies unless at extreme densities, but lives off of the butterfly and replicates itself in order to infect further caterpillars, butterflies and continue the cycle.

It does, however, have consequences. Studies by Sonia Altizer and Karen Oberhauser at the University of Minnesota have shown that butterflies infected with *O. elektroscirrha* have shorter wingspans and weigh less than uninfected butteflies, and heavily infected males had shorter life spans and reduced reproductive success. Intriguingly, they also found a correlation between the prevalence of *O. elektroscirrha* and migratory behavior: populations with higher infection rates had smaller Monarchs who were unable to fly as far as those populations with lower infection rates.

Finally, pathogens such as fungi, viruses and disease organisms also take their toll on butterfly survival. For example, nuclear polyhedris viruses (NPVs) are devastating pathogens that grow in the gut system of caterpillars and eventually kill almost 100 percent of infected individuals. Outwardly there may be no indication that a caterpillar is infected until they stop moving and seemingly dissolve from the inside out. Similarly, fungal spores, naturally occurring bacteria such as *Bacillus thuringiensis* (*Bt—See Pollen, Corn and Monarchs, on page 68*), and other disease organisms, kill large numbers of immature insects. Unfortunately, as with predators, we usually know too little about specific pathogenic threats to Monarchs.

Herbicides and Pesticides

Pesticide and herbicide use is still one of the most important threats to breeding and migrating Monarchs. The statistics—billions and billions of kilograms and liters of this pesticide or that herbicide—are scary, to say the least. Even modern shifts to organic methods of growing and pest control and the use of more targeted biocides (often biological control methods using principles and toxins from naturally occurring sources, such as *Bt*) have not stemmed the tide of pesticide use.

Unfortunately, the majority of crop plants that we grow are veritable monocultures—row upon row of genetically identical plants selected to maximize yield. The problem is that without genetic variation there is no way for identical plants to fight pathogens without the generous use of pesticides, or the incorporation of toxins within the crops themselves. Today we have chemical companies that own patents on specific hybrid strains of common crops setting



Predators of the Monarch are legion in North America, and can assume many different forms. A Queen larva succumbs to a disease pathogen (above), a Monarch pupa is parasitized by Tachinid flies (inset), and a spider cuts a Monarch loose from its web (opposite). Curiously, the spider will not eat the Monarch after it learns that the butterfly is poisonous.



POLLEN, CORN AND MONARCHS

n 1999, a trio of researchers at Cornell University published a research paper in the journal *Nature* revealing that some hybrid corn plants, genetically modified to include genes from the pathogenic Bacillus thuringiensis (Bt) as an anti-herbivore defense against foliage-feeding corn earworms and other herbivores of corn, were capable of releasing pollen that included the Bt toxin. Because corn is a wind-pollinated species, pollen carrying the toxins was reported to have drifted and deposited on nontarget plants at some distance from the source. These non-target plants included the milkweed host plants of Monarchs, and the researchers reported that caterpillars which ate leaves dusted with pollen were more likely to die than those that fed on leaves with corn pollen from unmodified plants or leaves without pollen.

The *Nature* report was abstracted and reported far and wide, creating a controversy in the popular

press with the Monarch and genetically modified organisms (GMOs) at its core. It was quickly interpreted (or misinterpreted, as we will see) as direct evidence that humans should "stop playing God" with the genetics of living organisms. Ethical and philosophical considerations aside, how much of an impact could what rapidly became known as "*Bt* corn" have on the Monarch?

A number of studies to confirm and verify the results of the Cornell study—which some complained had serious interpretation and methodological problems—were undertaken. A second report on the effects of *Bt* corn pollen on the Monarch (actually conducted a year before the Cornell paper but published afterward) included an assessment of natural "pollen loads" on potted plants placed near corn fields and used laboratory assays of Monarch caterpillars on leaves dusted with pollen to determine mortality. They conclud-

schedules for the application of specific pesticides—pesticides that they themselves manufacture—at specific times in order to maximize or even obtain a yield. And it's not only big business farms and chemical company profits individually we may think that we contribute very little to the problem but combined we probably use just as much pesticide on our backyard gardens. Suffice it to say, that pesticide use is rampant throughout the breeding range and migratory routes of the Monarch.

Monarch mortality is also being seen as an indirect consequence—collateral damage, if you will—of pesticide use against other targets, such as control of the imported gypsy moth. These effects are liable to increase with the advent of West Nile virus, a mosquito-borne human pathogen that has recently been

ed that there was significant mortality of Monarch caterpillars. Others in the scientific community were quick to point out, however, that the particular hybrid strains used included one with pollen toxin levels known to be more than 50 times higher than those in other studies.

Subsequent reports, controlling for all of the potential error sources that earlier papers were criticized for, eventually determined that the impact of pollen from the most commonly planted strains of *Bt* corn was essentially nonexistent. Pollen did not travel nearly as far, nor accumulate to high levels, on milkweeds as was supposed. Further, the amount of *Bt* toxin in the pollen was much lower and had little impact when ingested by Monarch caterpillars feeding in areas adjacent to the corn fields. Still, there are some who do not accept the subsequent reports and have elevated the Monarch to the status of an icon for the anti-GMO lobby.

There is little doubt, at the end of this tempest in a teapot, that what was once a little-used, naturally-occurring "biological control pesticide" is now a major pesticide due to its incorporation into so many crop plants. Further effects, although not anticipated, cannot be completely ruled out.

This is not to say that the "*Bt* corn scare" didn't have some effects on the Monarch. Surprisingly, these effects are positive, because as a consequence of the scare a number of intensive studies were conducted to determine how many milkweeds and Monarchs were found in or near cornfields. The result has been a worthwhile increase in our knowledge of the size and extent of the Monarch and milkweed populations through a large proportion of the Monarch breeding range. There is a silver lining to every cloud.

introduced to North America and is now here, I'm afraid, to stay. A recent example of the collateral effect of mosquito spraying was the spraying of permethrin in Gaylord, Minnesota. This small town of 2,000 had permethrin sprayed late in the day, unfortunately at levels higher than those recommended by the manufacturer, and that evening and the following day dying Monarchs were seen by the residents. Subsequent analysis of the dead butterflies confirmed that they contained lethal doses of the pesticide.

The direct action of pesticides on Monarchs is pretty easy to understand: contact in sufficient quantities kills the growing caterpillar, pupa or butterfly; however, there are probably also sub-lethal effects (for example, on lifespan or reproduction) that indirectly impact Monarch populations or migration.





Pesticides and herbicides are two of the most formidable threats to the Monarch in North America. Whether natural or chemical, pesticides directed at other targets, such as gypsy moths or mosquitos, can be deadly to Monarchs, while indiscriminate herbicide use deprives the butterflies of milkweed and flowers for nectaring. Herbicides, though, work almost entirely indirectly. Milkweed plants sprayed with herbicides may die, and any caterpillars present may starve, but the real effect of herbicides is habitat loss through degradation. Kilometers and kilometers of roadsides are sprayed with herbicides every year as an economical alternative to mowing regimes. Regardless of source or reason, habitat loss remains the main threat facing Monarchs.

Finally, while we have considered the effects of global warming as an environmental concern, the ultimate cause of warming trends is pollution of the environment by gases released as the products of combustion, specifically carbon monoxide, carbon dioxide and ozone. The cumulative but indirect effect of these compounds is to increase the heat retention of the atmosphere, but could there also be direct effects on Monarchs? There are negative effects of ozone on milkweeds and because milkweeds grow along roadsides and the automobile is the most common and prolific polluter that we know, there are likely other effects. The short answer—but the only one we have—is that we just don't know.

Genes and Generations

The issues, threats and problems that face Monarchs and their obligate larval host plants should not be viewed in isolation. Remember that we're talking about four or five *generations* of butterflies here. The generation that survived the winter in Mexico had encountered all of these potential sources of mortality on their journey south and will encounter some of them again as they begin to recolonize the continent. The first spring generation will contend with these issues through their immature stages in northern Mexico and Texas before they too continue the journey north, followed by the second spring generation that must pass through increasingly populated regions and the attendant problems of human competition for land and dominance on its way to the limit of its range expansion.

Similarly, the one or two resident summer generations (depending on whether they are at the southern or northern portions of the breeding range) will have to contend with these issues. These generations are the very antithesis of migratory, since mark-release-recapture studies have shown that these Monarchs stay in one place. Yet despite not traveling over large distances, they are not one whit less endangered. Finally, the migratory generation reappears, again dealing with the trials and tribulations of surviving the immature stages, but also having to survive the exceedingly long migratory flight to return once again—for the first time in their case—to roost in the mountains of the *Sierra Volcanica Transversal* in central Mexico.

What is most fascinating about the multi-generational nature of the eastern North American Monarch's migration is the genetic structure of the populations. Consider for a moment how much or little you resemble your parents and, if you have children, how much or little they resemble you. Every generation is different because parental genotypes mix to form the progeny genotype and not all of any one parent's genes are expressed in their offspring. Now consider that there are four or five *generations* of Monarch butterflies between migrant generations.

There are two intriguing forces at work here. The first and most obvious is that *all* of the butterflies in the migratory generation—the entire population mates virtually at the same place and time. A thorough mixing of all available genes is completely assured under these conditions, because the chances of any individual butterfly mating with a relative are greatly reduced. On top of this, females frequently continue mating as they travel northward, often mating four or more times, and the multiple paternity of their offspring further dilute and mix the genes.

At the other end of the range, however, there is evidence of genetic differentiation through inbreeding, that is mating between relatives that reinforces some traits in some sub-populations that are different from those in other subpopulations. Yet even five generations is too short a time to generate major changes, and even if there were any minor genetic variations, they would be erased every five generations during the mixing of individuals from all over the breeding range in the fall migration and subsequent random mating during the breakup of the overwintering roosts.

The end result of all this is what has been called a "general-purpose genotype." All of the individuals in the entire population carry a microcosm of all of the genes in the entire population. This kind of variation is generally associated with species that are successful in a wide variety of conditions, including unpredictable changes in environment. It is, I think, one of the potential saving graces of Monarch conservation since it suggests that any genetic bottlenecks—the reduction of the population to a relatively few breeding individuals and the loss of genetic variation not present in those individuals—are less likely to be of major consequence.



Every year scientists tag Monarchs in an effort to monitor changes in the population and migration patterns. Assisting in a tagging project is one way you can help Monarch conservation efforts.



The migration of the Monarch butterfly, Danaus plexippus (Nymphalidae). Individuals from their late-summer range in Canada must travel up to 2,500 miles (4,000 km) to reach the overwintering grounds in central Mexico.