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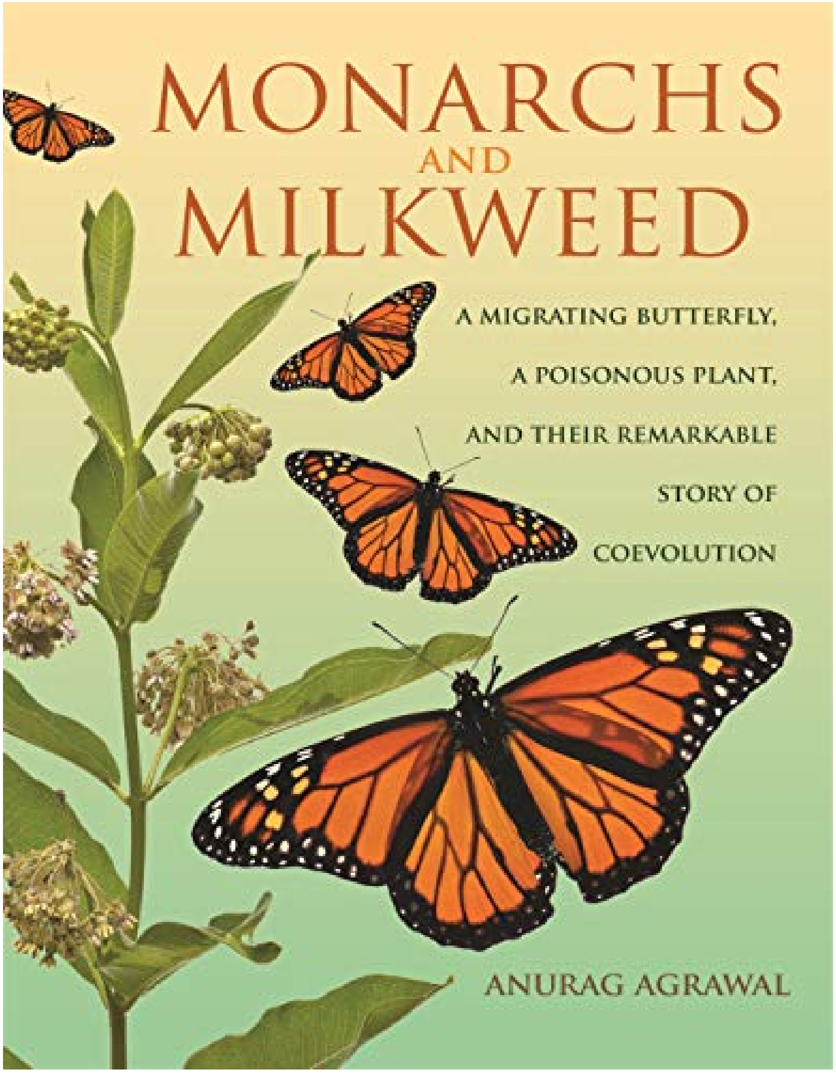
Monarchs and Milkweed: A Migrating Butterfly, a Poisonous Plant, and Their Remarkable Story of Coevolution

by
Anurag Agrawal



Synopsis

The fascinating and complex evolutionary relationship of the monarch butterfly and the milkweed plantMonarch butterflies are one of nature's most recognizable creatures, known for their bright colors and epic annual migration from the United States and Canada to Mexico. Yet there is much more to the monarch than its distinctive presence and mythic journeying. In Monarchs and Milkweed, Anurag Agrawal presents a vivid investigation into how the monarch butterfly has evolved closely alongside the milkweed—a toxic plant named for the sticky white substance emitted when its leaves are damaged—and how this inextricable and intimate relationship has been like an arms race over the millennia, a battle of exploitation and defense between two fascinating species.The monarch life cycle begins each spring when it deposits eggs on milkweed leaves. But this dependency of monarchs on milkweeds as food is not reciprocated, and milkweeds do all they can to poison or thwart the young monarchs. Agrawal delves into major scientific discoveries, including his own pioneering research, and traces how plant poisons have not only shaped monarch-milkweed interactions but have also been culturally important for centuries. Agrawal presents current ideas regarding the recent decline in monarch populations, including habitat destruction, increased winter storms, and lack of milkweed—the last one a theory that the author rejects. He evaluates the current sustainability of monarchs and reveals a novel explanation for their plummeting numbers.Lavishly illustrated with more than eighty color photos and images, Monarchs and Milkweed takes readers on an unforgettable exploration of one of nature's most important and sophisticated evolutionary relationships.

Look inside the book

Monarchs and MilkweedMonarchs and MilkweedA MIGRATING BUTTERFLY, A POISONOUS PLANT, AND THEIR REMARKABLE STORY OF COEVOLUTIONAnurag AgrawalPRINCETON UNIVERSITY PRESSPRINCETON AND OXFORDPublished by Princeton University Press, 41 William Street, Princeton, New Jersey 08540In the United Kingdom: Princeton University Press, 6 Oxford Street, Woodstock, Oxfordshire OX20 1TRJacket photos by Ellen WoodsLibrary of Congress Cataloging-in-Publication DataNames: Agrawal, Anurag A.Title: Monarchs and milkweed : a migrating butterfly, a poisonous plant, and their remarkable story of coevolution / Anurag Agrawal.Description: Princeton : Princeton University Press, [2017] | Includes bibliographical references and index.Subjects: LCSH: Monarch butterfly. | Milkweed butterflies. | Milkweeds. | Coevolution.Classification: LCC QL561.D3 A47 2017 | DDC 595.78/9—dc23 LC record available atBritish Library Cataloging-in-Publication Data is availableThis book was supported in part by Cornell University's Atkinson Center for a Sustainable Future ()This book has been composed in Perpetua StdPrinted on acid-free paper. " Printed in China10 9 8 7 6 5 4 3 2 1CONTENTSILLUSTRATIONS

Monarchs and Milkweed

CHAPTER 1
Welcome to the Monarchy

You who go through the daylike a wingèd tigerburning as you flytell me what supernatural lifeis painted on your wingsso that after this lifeI may see you in my night—Homero Aridjis, “To a Monarch Butterfly”

The monarch butterfly is a handsome and heroic migrator. It is a flamboyant transformer: an egg hatches into a white, yellow, and black-striped caterpillar; then a metamorphosis takes place inside its leafy-green chrysalis, which is endowed with gold spots; the adult butterfly that emerges flaunts orange and black (fig. 1.1). In the monarchs’ annual migratory cycle—perhaps the most widely appreciated fact about them—individual butterflies travel up to five thousand kilometers (three thousand miles), from the United States and Canada to overwintering grounds in the highlands of Mexico. After four months of rest, the same butterflies migrate back to the United States in the spring. Come summer, their children, grandchildren, and great-grandchildren will populate the northern regions of America.But there is much more to the monarch’s story than bright coloration and a penchant for epic journeys. For millions of years, monarchs have engaged in an evolutionary battle. The monarch’s foe in this struggle is the milkweed plant, which takes its name from the sticky white emissions that exude from its leaves when they are damaged. The monarch-milkweed confrontation takes place on these leaves, which monarch caterpillars consume voraciously, as the plant is their exclusive food source. Milkweeds, in turn, have evolved increasingly elaborate and diversified defenses in response to herbivory. The plants produce toxic chemicals, bristly leaves, and gummy latex to defend themselves against being eaten. In what may be considered a coevolutionary arms race, biological enemies such as monarchs and milkweeds have escalated their tactics over the eons. The monarch exploits, and the milkweed defends. Such reciprocal evolution has been likened to the arms races of political entities that stockpile more and increasingly lethal weapons.FIGURE 1.1. The monarch butterfly in three stages: (a) a caterpillar eating a milkweed leaf, (b) a chrysalis undergoing metamorphosis, and (c) an emerging butterfly before it expands its wings.This book tells the story of monarchs and milkweeds. Our journey parallels that of the monarch's biological life cycle, which starts each spring with a flight from Mexico to the United States. As we follow monarchs from eggs to caterpillars, we will see how and why they evolved a dependency on milkweed and what milkweed has done to fight back (fig. 1.2). We will discover the potency of a toxic plant and how a butterfly evolved to overcome and embrace this toxicity. As monarchs transition to adulthood at the end of the summer, their dependency on milkweed ceases, and they begin their southward journey. We will follow their migration, which eventually leads them to a remote overwintering site, hidden in the high mountains of central Mexico. Along the way, we will detour into the heart-stopping chemistry of milkweeds, the community of other insects that feed on milkweed, and the conservation efforts to protect monarchs and the environments they traverse.To be sure, this story is about much more than monarchs and milkweeds; these creatures serve as royal representatives of all interacting species, revealing some of the most important issues in biology. As we will see, they have helped to advance our knowledge of seemingly far-flung topics, from navigation by the sun to cancer therapies. We will also meet the scientists, including myself, who study the mysteries of long-distance migration, toxic chemicals, the inner workings of animal guts, and, of course, coevolutionary arms races. We will witness the thrill of collaboration and competition among scientists seeking to understand these beautiful organisms and to conserve the species and the ecosystems they inhabit.FIGURE 1.2. An unlucky monarch butterfly caterpillar that died after taking its first few bites of milkweed, the only plant it is capable of eating. In a violent and effective defense, toxic and sticky latex was exuded and drowned the caterpillar. A substantial fraction of all young monarchs die this way.FROM SIMPLE BEGINNINGSFrom a single common ancestor, milkweeds diversified in North America to more than one hundred species. And the monarch lineage is no slouch, with hundreds of relatives we call "milkweed butterflies" throughout the world. Although monarchs are perhaps best known in the northeastern and midwestern United States, they occur throughout North America, and self-sustaining populations have been introduced to Hawaii, Spain, Australia, New Zealand, and elsewhere (fig. 1.3). Interactions between butterflies and milkweeds now occur throughout the world, but this account focuses primarily on what happens in North America. The reason is quite simple: eastern North America is where the monarch (Danaus plexippus), considered by most to be the pinnacle of milkweed butterflies, coevolved with milkweeds.The monarch's annual cycle in eastern North America involves at least four butterfly generations, with individuals crossing international borders several times. In spring, butterflies migrate from Mexico to the southern United States. Flight is fueled by nectaring on flowers and is punctuated by laying eggs on milkweeds. To grow and sustain each generation, milkweed is the only food needed. Three cycles—from egg to caterpillar, to chrysalis, to butterfly—occur as monarchs populate the northern United States and southern Canada each summer. And while nearly all mating, egg-laying, and milkweed eating occurs in the United States and Canada, each autumn monarchs travel to Mexico. At the end of summer, southward migrating monarchs fly thousands of kilometers and then rest for some four months before returning to the Gulf Coast states in the following spring. How and why they do it is a story that continues to unravel, and it no doubt will keep scientists busy for centuries.The energy that builds a monarch butterfly's body ultimately comes from plants—as it does for all animals. For most butterflies and moths (collectively, the Lepidoptera), the caterpillar stage is essentially a leaf-eating machine. Perhaps it is not surprising then, that caterpillar feeding has led to the evolution of armament (or "defenses") in plants. The leaves of nearly all plant species are not only unappetizing to most would-be consumers; they are downright toxic. Milkweed's toxicity has long been known, and foraging on milkweed has surely killed countless sheep and horses. Most other animals avoid this milky, sticky, bitter weed, and yet monarchs came to specialize on it. While the toxic principles of milkweed keep most consumers at bay, monarchs and a few other insects have craftily adapted to the plant. Humans have used the chemical tonic of milkweeds as medicine for centuries, and so too have monarchs exploited their medicinal properties—at least at low doses. As the great Renaissance scientist Paracelsus noted five hundred years ago, "dose makes the poison"; there is often a fine line between poison and medicine. Much of this book is devoted to unraveling the evolution of poisonous and medicinal properties in plants that are habitual fodder for animals.The evolutionary war waged between monarchs and milkweed is a product of their intimate relationship. Monarchs not only tolerate milkweed's toxicity but have evolved to put it to work. For more than a century, insect enthusiasts have observed that most bird predators leave monarchs alone, presumably because their bright coloration signals a toxic body. Nonetheless, monarchs are not free of enemies. Flies and wasps consume them from the inside and eventually burst out. Tiny protozoan parasites infect their bodies, and monarchs medicate themselves with milkweed's toxins.FIGURE 1.3. The worldwide distribution of monarch butterflies. Although native to the Americas, they have been introduced to the South Pacific, Australia, and Spain over the past few hundred years. The introduction of weedy milkweeds to these new regions, mostly the tropical milkweed Asclepias curassavica, preceded the establishment of monarchs. Monarchs are most abundant in North America.The milkweed plant is not a passive victim being devoured by monarchs. When the plant is attacked, its entire physiology, expression of genes, and toxicological apparatus kicks into high gear like an immune system. Milkweeds may lack an animal's central nervous system, but they possess all the other attributes common to the sessile sugar factories we call plants. They actively engage in strategies that defend against, tolerate, and when possible, manipulate insect enemies like the monarch butterfly.While some mysteries of monarchs and milkweeds were only recently solved, much of what I present about the interaction between monarchs and milkweeds was reasonably well known (or at least hypothesized) more than a century ago (fig. 1.4). Searching through old newspapers, one can find beautiful accounts of their relationship. Although the classification of the monarch butterfly has changed over the past 150 years, the intimate interaction with milkweed was observed from the very beginning. Monarch "plagues" have been reported for at least as long, frightening entomophobes (people afraid of bugs). Nonetheless, because milkweed is sometimes considered an undesirable weed, an abundance of monarchs was also said to be beneficial by entomologists who knew the insect, as it might control the plant. There were newspaper reports of "Monarch Invasions from Canada" (as they migrated south past Rochester, New York) as early as the 1880s. Although there was some controversy about whether the butterflies migrated long distances, it was solidly hypothesized early in the twentieth century that this insect followed the seasons, south in the autumn, and with multiple generations moving northward each spring. How and why they migrate, and how and why they feed exclusively on milkweed, were discoveries made over the next hundred years. Honestly, they are not fully solved mysteries, but we have made great progress, and this book is about revealing the science behind these discoveries.Monarchs have also been proposed as a sentinel, whose health as a species may be a “canary in a coal mine” for the sustainability of the North American continent. They travel through vast expanses, tasting their way as they go. Although they tolerate milkweed poisons, they are highly susceptible to others, especially pesticides. Summer and winter climates are likely the key drivers of the monarch’s annual migration: feed on spring and summer milkweed foliage, follow the season north as it is progressively unveiled, rest in the chill mountain air in winter. Their time in Mexico is delicately balanced between being physiologically active, but cool, not burning precious energy before spring arrives. Our changing climate is certainly affecting monarch butterflies, although we are just beginning to understand the severity of these effects.FIGURE 1.4. A newspaper article about the monarchs’ migration from the Washington Post, September 17, 1911.In some respects, human activities have enhanced habitat for milkweeds and monarchs north of the overwintering grounds. Logging and agriculture have been good for monarch populations in some regions, like the eastern United States, where these pursuits likely made milkweed and its associated butterflies much more abundant. However, farming surely destroyed much of the midwestern prairie, where milkweed had previously been prolific. Now the same processes, combined with the indirect influences of other human activities, have been suggested as drivers in the decline of monarch butterfly populations. I evaluate what is known about the causes of monarch and milkweed ups and downs toward the end of this book. If they are truly sentinels, then much more than the sustainability of monarchs is at stake, and careful study of their biology—past, present, and future—is in order.GETTING INFECTEDHow ecological interactions—plants and insects, monarchs and milkweeds—caught my attention is a story in and of itself. I grew up in a fairly rural area of suburban Pennsylvania, where fields of red clover and foxtail grasses were common, and my brother and I were encouraged to spend much of our time outside. Vacations were spent camping; my mother was, and continues to be, an insatiable gardener; and the corn fields growing behind my home prompted me to want to be a farmer. As a college student at the University of Pennsylvania, I felt the bliss of self-discovery, yet also the pressures of being a child of immigrant parents who were unfamiliar with most academic endeavors outside of medicine and engineering. My parents’ proviso concerning my college education was that, in addition to exploring my interests in social science and the humanities, I take introductory science and math classes, so as not to close too many doors. Fair enough.As a sophomore, I decided to take introductory biology. But, because the lecture halls were limited in their seating, and because many colleges feel pressure to have smaller classes (after all, small classes enhance students’ learning, as well as college rankings), there were two offerings of the course that semester—similar classes, covering much the same material, but taught by different professors. To choose, I did what many students did, and still do: I consulted what was known as a “skew guide,” a “for the students, by the students,” survey of courses that outlined the degree of difficulty, what was liked and disliked by students who had taken the course previously, and unashamed caricatures of the esteemed faculty—the clothes they wore, comments about their hygiene, and notes about their traits, usually having little to do with their ability to impart scholarly information. Sad but true, what sealed the deal for me was the characterization of one of the professors: “typically comes late to class and leaves early.” I actually don’t remember if that ended up being true, but the course, and his approach to biology, caused a profound shift in my own development as a student. Dr. Daniel Janzen presented biology as a set of stories, far stranger than any science fiction I had read. Biology was a series of mysteries that could be solved by careful observation and clever manipulation. Biodiversity was presented as a bottomless mine of species and interactions that had been shaped by both millions of years of evolution and the now dominant species on the planet, Homo sapiens (fig. 1.5).FIGURE 1.5. In a memorable lecture on butterflies and poisonous plants, Dr. Janzen showed this slide depicting the unpalatability of milkweed. The toxic plant flourished under grazing pressure because it was avoided by horses (right side of the fence). But where horses were absent (left), milkweed was less abundant and suffered from competition with grasses.A recurring theme of the course and the professor's favorite organisms for study were plants that were damaged by insects. Insects eating plants? What about the charismatic megafauna: lions, tigers, and sharks? Or at least buffalos and birds? Now that I am a professor, I annually teach a course called "Chemical Ecology" with several faculty colleagues at Cornell University. In this course we analyze how chemicals in the natural world mediate interactions between species. Why are chilies and horseradish spicy? How do monarch butterflies gain their toxicity? And, are there really human pheromones? Yet, our lectures often focus on insects eating plants. Comments from students in our course evaluations occasionally plead, "Enough with the caterpillars already!" Yet it is the abundance, diversity, and general importance of insect-plant interactions that motivate our course, as well as my own fascination and research focus on monarchs and milkweeds.ARTHROPOD-PLANT INTERACTIONSWhat can little creatures like monarch butterflies and their vegetarian habits teach us about nature? First, the source of essentially all of the energy that powers an animal—really, any food chain—comes from plants. They constitute an exclusive group of organisms that can process nonliving matter and turn it into the energy that is needed for life. That process is photosynthesis, and that energy is sugar. Plants take sunlight, carbon dioxide from the air, and water, and through a chemical reaction produce oxygen and sugar. That sugar powers life on earth. Sure, we don't typically think of lions, tigers, and sharks as relying on plants. But they do. They eat other animals that survive by eating plants. Meanwhile, plants "eat" earth, wind, and sun. As such, plants make up the largest fraction of living matter (what biologists call "biomass") on the planet. Milkweed is but one of hundreds of thousands of plants species, yet it is an excellent representative to teach us about biology.$6CO_2 + 6H_2O$ + photons !' $C_6H_{12}O_6 + 6O_2$carbon dioxide + water + light energy !' sugar + oxygenSecond, there are two pathways by which plant energy enters a food chain: as compost and as salad. Most of it, probably 80 percent or so, enters the food chain as rotting compost. As leaves fall off plants, microbes, worms, and microarthropods shred it, transform it, and make it available as broken-down food and nutrients for others. The rest, about 20 percent of plant material, enters the food chain fresh, as a "salad." Monarchs are but one of the millions of leaf-eating species that can teach us about the consumption of living plant tissues by animals. And, yes, although it is true that zebras and porcupines are charismatic megafaunal herbivores (big mammals that eat plants), in other ways, insects like monarchs dominate the scene (fig. 1.6).FIGURE 1.6. The Bioscape, where taxonomic groups are drawn proportional to the number of currently known species. In this diagram, the monarch represents all insects. Among the 2 million described macroscopic species (visible to the naked eye), about one quarter are herbivorous insects. Yet, our best guesstimates of the actual number of herbivorous insects on the planet range from 2 million to 5 million species. As we discover the rest of the species, plants are likely to constitute about 10 percent of the total number of species. Even by the most generous estimates, all vertebrates combined (including mammals, birds, fish, reptiles, and amphibians) would hover around 2 percent of species, and 70 percent of species are likely insects (about half of which are herbivorous). Accordingly, in terms of the source of the planet's overall energy, biomass, and biodiversity, plants and herbivorous insects play a dominant role.The third reason for a focus on insects and plants is quite practical. These organisms are typically easy to cultivate in large numbers, in relatively small spaces, and with relatively little interference from animal rights activists. The consequence for scientists is that we can work toward strong inference in our studies. “Strong inference,” a term introduced by a biophysicist and philosopher of science, J. R. Platt, in 1964, refers to going beyond single factors as explanations of natural phenomena, and going beyond correlations as explanations for the causes of patterns. Many correlations are statistical associations that have no “causal” basis. The variable on the x axis of a graph, although correlated with a variable on the y axis, is not the cause of variation in the variable on the y axis. Take, for example, the strong positive correlation between the per capita consumption of chocolate in a country and the number of Nobel laureates from that country. To quote from a tongue-in-cheek article published in the New England Journal of Medicine: “[We] estimate that it would take about 0.4 kg of chocolate per capita per year to increase the number of Nobel laureates in a given country by 1.” To evaluate correlations rigorously, and hence to promote strong inference, one typically needs large numbers of study subjects, the testing of alternative explanatory factors, and a critical experiment. The abundance of insects on plants, along with the ability to raise them in both the laboratory and field, makes them ideal scientific subjects. Distinguishing between correlation and causation is critical to our understanding of the biology and conservation of monarchs and milkweeds. Turing back to our study of chocolate: countrywide spending on science also correlates with per capita income, the latter of which correlates with chocolate consumption (at least in the Western world). Even so, I would happily participate in a controlled study to determine the influence of chocolate consumption on scientific discoveries.Given the attributes of insects and plants, it is perhaps not surprising that their study has become a bit of cottage industry among biologists. We even have a specific journal dedicated to publishing scientific studies on insect-plant interactions. Well, to be honest, it is called Arthropod-Plant Interactions, so as to include studies of related creatures with more than six legs, such as spiders, mites, millipedes, and centipedes. The main point, however, is that in addition to their general abundance, diversity, fascinating biology, and tractability of study, these insect-plant systems have become a general model for understanding biology. Given the millions of species on the planet, biologists make progress through the in-depth study of several “model systems” that intensely examine a few selected organisms, with the hope of generalizing to other systems. Sometimes these “models” are specific species (like the lab rat). In other cases, however, the models may be habitats or groups of species that have their own ecologies.Monarchs and milkweeds have proven to be an excellent model system through which we can understand the coevolution and conservation of species. Like all plants, milkweeds have an arsenal of toxins, evolved by natural selection, to ward off pesky herbivores. Like all herbivores, monarchs have a diverse portfolio of tolerances and strategies that leave them undeterred from feeding on their food. And all animals have their own enemies, predators, parasites, and microbial infections. Monarchs are no exception, and yet the detailed study of their relationships has revealed a role for milkweed’s toxic properties in the interaction between monarchs and their enemies. The monarchs’ spectacular form and flight, although extravagant, demonstrates the lengths to which natural selection can go. And because of the food and habitat needs of the monarch along its annual migratory cycle, monarchs have now become important in understanding general principles of species conservation. Monarchs and milkweeds have served as an important icon for debates and concerns about genetically modified organisms, climate change, and environmental issues more broadly.FINDING MONARCHS AND MILKWEEDSInspired by Professor Janzen’s introductory biology class, fueled by a newly found passion for studying insects on plants, and advised to find one of the big state universities (“the land grant colleges,” as they are called), I ended up pursing a PhD at the University of California, on the Davis campus. I landed at UC Davis probably because of the confluence of several factors: it was far enough from home that it sparked some sense of exotic mystery; it provided the opportunity to study with a talented and beloved mentor, Dr. Richard Karban, who remains a friend and inspiration; and it had one of the top programs in ecology and evolutionary biology. My parents were slightly befuddled, if not worried, by this choice. The university was not a big name school, it was far from home, and, after all, I was leaving the traditional lines of inquiry to become some sort of bug doctor.It was not until near the end of my time at Davis, however, when my wife, Jennifer Thaler, and I had both secured faculty jobs in the Botany Department at the University of Toronto, that a path first led me to the world of monarchs and milkweeds. As I looked forward to starting new research projects at a new job, I found it both an exciting and daunting challenge. How to pick a fruitful set of organisms to work on, one that would provide scientific insights, prove amenable to discovery, and perhaps above all, promote inspiration? My friend, collaborator, and graduate student colleague, James Fordyce, known to most as Jimmy, and to some as Uncle Jimmy, suggested that I consider working on monarchs and milkweeds (fig. 1.7). Now a professor at the University of Tennessee, he had worked on milkweed insects for his master's degree. The reasoning behind Jimmy's proposal is worth explaining, because it directly relates to what makes monarchs and milkweeds ideal study subjects.The first attribute of monarchs and milkweed is that they have long been the recipients of love and affection from all kinds of people. And this love is expressed is various ways: by observations in nature, hands-on husbandry, the buying and selling of butterflies and seeds, digital information, symbols in the logos of organizations, and scientific study. Hundreds of thousands of monarchs are reared each year in classrooms and homes in the United States alone. At least as many are reared by butterfly breeders for sale and releases at weddings and other special occasions. Any search of "monarch butterfly" on the Internet yields hundreds of thousands of websites. Over the past twenty years, the New York Times alone has published more than one hundred articles about monarchs, averaging one every two to three months. Monarchs have become logos and symbols for organizations far and wide, including the Union of Concerned Scientists, many K–12 schools, the non-GMO project, and numerous corporations whose businesses range from manufacturing to banking. And, finally, a recent survey of thousands of Americans revealed that, collectively as a nation, households are willing to donate nearly $5 billion to aid in the conservation of monarch butterflies. The study revealed a willingness to donate on par with many endangered vertebrate species (although not as much as for bald eagles, elephants, and gray whales).FIGURE 1.7. A typical summer sight in eastern North America—a monarch caterpillar getting ready to feast on the common milkweed, Asclepias syriaca.As a result of public interest and much scientific study, we know a tremendous amount, not only about these two organisms' natural history, but also about their coevolutionary basics. Common milkweed was transplanted and established in Europe as a possible (failed) source of rubber for tires and fluffy fill for pillows. Milkweeds are toxic plants that most animals do not eat. Monarchs cannot live without the milkweeds; it is the only food they eat. But milkweeds and monarchs are both toxic. The plant poisons, which have been used medicinally for hundreds of years, are taken up by monarchs and ward off bird predators. The monarch migration is legendary, mind-boggling, and indefatigable. The list goes on. This plant-insect interaction brings together a renowned butterfly, attractive plants, and a rich vein of history, biology, and ecology.Second, what makes monarchs and milkweeds good scientific subjects is advertised by the plant's common name. How I have lamented the "weed" in the name "milkweed." As Ralph Waldo Emerson once quipped, a weed is simply "a plant whose virtues have not yet been discovered." Other previously used names for this beautiful plant include swan plant and silky swallow-wort, but none other than milkweed stuck. Nonetheless, the weediness, at least of common milkweed (Asclepias syriaca), and the weediness of monarchs themselves, is an attribute that makes them great biological subjects because they are abundant. The insects and plants alike are easy to spot. The butterflies are colorful, typically not elusive, and active during the daylight hours. These species make the process of doing science—rearing lots of them, screening them for their traits and behaviors, finding them in the field, and grinding them up in the laboratory, an easier process. Although working on rare species is certainly an important task for ecologists, rarity presents a set of challenges before scientific investigation even begins.Third, both monarchs and milkweeds are native to North America. Biologists are often obsessed with this notion of "native," because it is thought to reflect some primordial state untouched by humans. Of course, nothing could be further from the truth. Even in the depths of the Ebook Tops or Siberia, humans have had an impact on most organisms and the habitats they occupy. Nonetheless, the native state of both partners in an ecological and evolutionary relationship makes it such that their behaviors and their biology were potentially shaped by their long-term interactions with one another. And monarchs and milkweeds do share a deep evolutionary history; they have existed together for a very long time, likely millions of years. Thus, we can interpret the ecology of this system through the lens of natural selection and coevolution.And finally, monarchs and milkweeds are a natural system with some balance between complexity and simplicity. Complexity can mean many things, but here I am thinking about diversity—of species, habitats, and interactions between species. Monarchs come from a group of some 6,000 brush-footed butterflies (in the family Nymphalidae), and many of the smaller grouping of 170 "milkweed butterflies" (in the tribe Danaini) interact with milkweeds (fig. 1.8). As I will discuss later, monarchs have an intimate association not only with milkweeds but also with microbial parasites, some of the other insects that eat milkweed, and a whole community of predators, from birds to spiders, and from stinkbugs to wasps. Not only does this diversity of potential interactions set the stage for endless scientific study, but the monarchs' yearly travels expose them to substantial variation in when and with what they interact. It is this diversity of species, interactions, and environments that they live in that is food for scientists: mysteries to be solved. Yet, for groups that are much more diverse, or associated with wildly different plants and parasites, the complexity can be overwhelming and make scientific progress quite slow.The complexity-simplicity balance also applies to the plants. Milkweeds come from a genus with about 130 species (given the genus name Asclepias by Carolus Linnaeus after the Greek god of medicine and son of Apollo, Asklepios). All Asclepias live in the Americas, with most living in Mexico and northward. It is not a tropical group of plants. The evolutionary sister group to Asclepias are more than 250 species in an African genus called Gomphocarpus (fig. 1.9). Of the American milkweeds, most are rare, and only a few species, like common milkweed, Asclepias syriaca, are highly abundant and noticeable in many environments. Species of milkweed do, however, inhabit some of the most diverse habitats available, from standing water to the driest of the dry deserts. And although most Asclepias live in open habitats, preferring full sun, a few species inhabit the forest shade. All are herbaceous (not woody) and perennial. Together these attributes point to a level of manageable complexity. That is, the plants have evolved from a single ancestor into many species, into many habitats, and with some variation in their ecology.FIGURE 1.8. The monarch arose from a group of about 170 physically similar, yet evolutionarily distinct species known as the milkweed butterflies (tribe Danaini). Shown is a phylogeny, or visual representation of the evolutionary relationships in this tribe. Note that most milkweed butterflies are not shown here (for example, there are twelve recognized species in the genus Danaus). Instead, representatives of each of the major groups are shown. The Ithomiini is the sister tribe to the Danaini and contains several hundred tropical species.FIGURE 1.9. A summary phylogeny showing the evolutionary relationships of the milkweeds in plant genus Asclepias (with about 130 recognized species in North America), here trimmed to show representatives of the major groups. No image of Asclepias californica is shown, and the representative of Gomphocarpus is G.fruticosus.Like all plants, these evolutionarily related species of milkweeds have their own special community of herbivores, giving the plants a predictable and well-defined group of insect enemies. And this too is an attractive attribute of the milkweeds for scientific study. Take the common milkweed, which is fed upon by eleven insects: three aphid species suck the phloem sap, two lygaeid bugs eat seeds, three different beetle species bore through the roots, tunnel in the stems, or eat the leaves, and a small flattish fly mines between leaf layers (see figures in chapter 7)—not to mention a moth and a butterfly species whose caterpillars chew the leaves. The insect community is complex yet simple. The complex part is that these insect herbivores have divvied up the plant, with different species eating different plant parts. Also, these insects span a tremendous taxonomic breadth, covering some 350 million years of evolutionary history. What I mean by this is that the diverse species of insects that now eat milkweed shared a common ancestor about 350 million years ago—the proto-insect. Over the past hundreds of millions of years, the insects' ancestors rampantly diversified, giving rise to honeybees, mosquitos, beetles, and butterflies, and many times independently distinct groups of these insects would colonize and adapt to eating milkweeds. Interestingly, these insect species are essentially all specialists. They are not omnivorous. They are not even adventurous. All they eat is milkweed. And therein lies the simplicity of monarchs and milkweed. The insects are confined to feeding on milkweed, and therefore we know where to find them; their dietary habits are well-defined; and they are decidedly pests on the plant.Our journey will now start in earnest by placing monarchs and milkweeds in the context of their stockpiling arms race. The nature of the monarch-milkweed interaction is simplified by the fact that monarchs are unquestionably pests and are not also pollinators or beneficial in any other way. Milkweeds must defend themselves. Early studies of this interaction led to the birth of a new scientific discipline called chemical ecology, which among other topics, tries to decipher the mechanisms and consequences of such arms races. Now that the field is maturing, it has created new scientific questions. What is most fascinating about monarchs is that they have cracked the milkweed's code of defense, forever changing the course of their coevolutionary interaction.CHAPTER 2The Arms RaceThere is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.—Charles Darwin, On the Origin of Species, final sentenceA monarch butterfly is perched on a milkweed flower, ready to take a sip of nectar. What a site of harmony in nature (fig. 2.1). But this butterfly is not a pollinator of milkweed. Instead, the butterfly is hoping to find a mate and then to have children that will devour the milkweed plant. Through evolution, the butterfly has adapted to exploit the plant, but there is nothing in it for the milkweed. And through a process called coevolution, the milkweed does not invite the monarch, but rather tries to ward it off. Their battle has been intense, so much so that back in Darwin's day, scientists used monarchs and milkweeds to advance new ways of looking at nature. Out of these insights, new disciplines of science emerged, including what we now call chemical ecology. What scientists eventually discovered was that the monarch-milkweed relationship initiates an extraordinary arms race.EVOLUTION AND COEVOLUTIONAll organisms on the planet, from ants and bacteria to cats and dogs, to elephants, figs, and giant saguaros, descended from a single, universal common ancestor. Darwin got it right when, in the last paragraph of his 1859 opus, On the Origin of Species, he wrote about this common ancestor and the subsequent and sustained evolution of diverse forms. This represents what is termed “macroevolution,” that which involves the generation (and loss) of distinct species. Such evolution is evident all around us, and many biologists spend their time interpreting the features of life in the context of evolution, because that is the only context in which biology makes sense.FIGURE 2.1. A male monarch butterfly perched on the flowers of common milkweed in the author’s front yard.The mechanism of Darwinian evolution is what we term “microevolution.” Microevolution is a change in the frequency of alternate forms of genes (or alleles) within a population of a single species, where these genes code for traits presumably important to the organism’s form and function. Through natural selection, the frequency of particular genes in a population changes. Think about the four human blood types (A, B, AB, and O), which are determined by a single gene. In some human populations, natural selection has favored a higher representation of particular forms of that gene, typically because different blood types are more or less resistant to particular diseases.In their simplest forms, micro- and macroevolution are beautiful, powerful, and commonplace at the same time. Polar bears’ white fur helps to camouflage them in the arctic, while their underlying black skin absorbs heat. Plants living in deserts have evolved many ways to conserve water, and animals that live in caves commonly lose their eyesight over evolutionary time. But evolution occurs not only with respect to the physical and chemical attributes of the environment (such as moisture, light, and temperature), but also in relation to the “biotic environment,” the other organisms with which a species interacts. Take, for example, the evolutionary origin of the revolutionary drug penicillin.Fungi that eat dead and decaying things, like the Penicillium molds that gave us penicillin, evolved to produce antibiotics to defend the resource they are eating from other tiny consumers, like bacteria. Each of the hundreds of species in the genus Penicillium produces distinct chemicals, most of which have been shaped by natural selection. Natural selection can be likened to a filter. As long as there is heritable variation in a population, natural selection can cause evolutionary change, because those individuals with advantageous traits are the ones who survive and successfully reproduce. Natural selection hones traits within populations of a species, and as populations diverge, macroevolution takes hold, allowing for speciation. In the case of Penicillium, diverse antibacterial toxins have evolved as a defense among the many species in this genus of fungi.Coevolution takes evolution in response to the biotic environment to the next level (fig. 2.2). When organisms interact, like the competing molds and bacteria, or the mutually beneficial relationship between flowering plants and pollinating bees, or the cat-and-mouse game of predators and prey, coevolution is possible. Coevolution is the reciprocal adaptation that occurs as species interact. The term “adaptation” means that the frequencies of particular beneficial genes in a population will increase. In coevolution, the changes are imposed by the interaction partner, say the cat imposing natural selection on the mouse. The evolutionary response to this selection may be that mice are better camouflaged or faster runners, as the more apparent or slower individuals will be removed from the population by predators. Critically, what makes coevolution different from everyday evolution is that coevolution involves reciprocity. That is, following adaptation by the mouse, say with faster and faster running speeds, natural selection is now imposed on the cat, causing the evolution of a more acute ability to sniff out or chase down mice.FIGURE 2.2. Two ways to envision coevolution. Left, reciprocal natural selection is illustrated as a continuous cycle. Right, the same process over time results in an “arms race,” with increased investment by the plant in defensive traits and by the insect in traits that exploit the plant. Note that there are other possible outcomes of coevolution not discussed here.The birth of coevolution as a concept, studied as the warfare between plants and herbivores, is credited most prominently to Ernst Stahl, who summarized his studies of snails and plants in 1888, only a few years after Darwin passed away. Stahl developed a theory of coevolution, and his framework set the stage for unraveling some of the mysteries of monarchs and milkweeds. His critical experiment was to take plant species that appeared to be avoided by snails in the field, to show that in the laboratory snails refused to eat these plants, and then to remove chemicals from the leaves using an extraction procedure (imagine soaking the leaves in alcohol overnight) and showing that those leaves were now palatable to the same snails. He interpreted his results in light of “reciprocal adaptation,” a very early reference to what we now call arms race coevolution. In particular, Stahl noticed that some snails were generalist feeders, and their ability to eat plants was enhanced by removal (extraction) of the plant’s chemical defenses. Alternatively, other snail species limited their diet to one or a few plant species—call them “specialist herbivores”—and these snails were observed to prefer plants in their intact state. It stood to reason that specialists were engaged in an arms race with the plants, eventually overcoming the plants’ defenses, and even using these “defenses” for their own purposes.MONARCHS, I DON’T REALLY NEED YOUHow species involved in interactions evolve and coevolve depends acutely on the nature of the interaction. If two species are strictly antagonists, then an arms race may ensue. Sometimes, however, species play dual roles, positive under some circumstances and negative in others. In this case, say if the monarch were both a beneficial pollinator and an herbivorous pest of the milkweed, perhaps the plant would not mount defenses. The benefits of butterfly pollination to milkweed could outweigh the costs of caterpillar herbivory. But here is where I must dispel a widely held myth about monarch butterflies. Milkweeds do not need monarchs, because the butterflies are simply no good as pollinators. Monarchs are strictly pests.Unlike many other coevolutionary relationships, that between monarchs and milkweeds is not symbiotic. Although many definitions of symbiosis exist, nearly all require the relationship to be close, and many definitions require the relationship to be mutually beneficial. From the monarch’s perspective, the relationship is intimate and beneficial. However, from the milkweed’s perspective, it is neither. The importance of this distinction will be increasingly apparent as we move forward, but for now let’s focus on the fact that monarchs frequently can be found collecting nectar from milkweed flowers. They drink nectar, but they are typically ineffective at pollinating the flowers. Without understanding this issue, we cannot understand the nature of the monarch-milkweed arms race.First, a bit of the birds and the bees—the reproductive biology of milkweeds. All milkweeds are perennial (they typically live and reproduce for many years). Despite their disappearance aboveground in the winter, the bulk of their biomass lives underground in the soil, stays dormant in the winter, and has plenty of stored reserves to power new shoots in the spring. Additionally, some, although certainly not all, milkweeds are clonal. That is, they send stems foraging underground and pop up new shoots when needed. This cloning of stems is in part responsible for common milkweed’s weediness. In addition, milkweeds reproduce sexually. They produce flowers, attract pollinators, send pollen to other plants, and receive pollen to fertilize ovaries and initiate the production of seeds (fig. 2.3). Most milkweeds do not accept their own (“self”) pollen; they need to receive pollen from an independent milkweed plant in order to successfully make a fruit full of seeds. Milkweeds cover a lot of bases with this way of life. They live many years with many opportunities for reproduction, which after all, is the main goal of all life. Where conditions are good and a particular plant is successful, milkweeds clone themselves locally. But, as a means to colonize new habitats, and to mix genes with mates, milkweeds engage in pollination and sex.Most important, the reproductive cycle of milkweeds does not include a role for monarchs. Although frequent visitors and drinkers of milkweed's nectar, monarchs are ineffective extractors and deliverers of pollinia (or pollen sacs). Milkweed flowers do not offer up loose pollen grains the way 90 percent of plants do. In fact, two groups of flowering plants, orchids and the subfamily that includes milkweeds (Asclepiadoideae) have evolved pollen packages called "pollinia," each with hundreds of tiny pollen grains. Milkweeds do not have loose pollen grains that can be collected by bees, rubbed onto insect abdomens, stuck to a butterfly proboscis (the tubular drinking mouthpart), or blown in the wind. So, for pollination to occur, the pollinia must be extracted from the milkweed flower and then inserted into the flower's female slit (or "stigmatic groove" in botanical terms). As my colleague Steven Broyles from the State University of New York at Cortland says, monarchs, with their long legs, simply don't contact the business-end of the milkweed flower.FIGURE 2.3. Pollination of milkweeds. When bees and other large insects in the order Hymenoptera visit milkweed flowers to drink nectar, (a) their legs slide near the flower's slit, and the bee's leg hairs often grab the top of the (b) wishbone-shaped pair of pollinia. (c) A successful removal of the pollinia results in its becoming attached to the bee's leg. Later, when the bee climbs over other flowers, a pollinium incidentally gets inserted into a slit, allowing for fertilization of the ovules by germinating pollen grains. (d) Monarchs, however (shown here on Asclepias tuberosa), are not good pollinators of milkweed. Because of their large size and way of sitting on flowers, monarchs uncommonly come into contact with the pollinia and slit.In other plant-insect associations, the same insect species may serve as a pollinator and also as herbivore of the plant. Although this is most famously known from the yucca plant and yucca moths, and figs and fig wasps, many plant-insect relationships follow suit. For example, the cabbage white butterfly (Pieris rapae), perhaps the most abundant butterfly in the world, not only pollinates mustards (relatives of cabbage in the family Brassicaceae), but also lays eggs on the plants after pollinating. Their larvae are voracious herbivores of mustard leaves and flowers. In such relationships, there is a conflict for the plant: how to attract and effectively use a pollinator without suffering from that pollinator's young consuming the plant. No such conflict exists in the milkweed-monarch matrix, so the plant can focus its energies first and foremost on defending against monarchs as pests.This nonpollinating aspect of monarchs is not widely appreciated. Although monarchs may successfully pollinate some plant species (perhaps in the sunflower family, Asteraceae), this phenomenon has not been well-studied, and they are surely unimportant compared with the myriad other flower visitors. Nonetheless, in a recent presidential memorandum (June 20, 2014), "Creating a Federal Strategy to Promote the Health of Honey Bees and Other Pollinators," Barack Obama singled out monarchs as the only species other than the honeybee (Apis melifera) to be named as an important pollinator. Because the monarch is not, however, a good pollinator, the arms race proceeds, with plants evolving defenses to reduce attack by monarchs and insect adaptations to overcome these defenses.EAT AND DON'T BE EATENThe arms race signifies a battle between species, although not one where they are simply stockpiling weapons to destroy each other. In the arms race between plants and herbivores, plants evolutionarily accumulate defenses while the herbivore evolves means to circumvent these defenses. For milkweeds, the plant has evolved several forms of armament, including potent toxic chemicals, and monarchs have evolved the physiological means to tolerate these chemicals. As coevolution proceeds, escalation in defense and offense reciprocally ensues (see fig. 2.2).But life isn't so simple. Every organism has its need for food and also has its own enemies to contend with. A major issue for most animals, really any organism, be it vegetable, animal, or germ, is to eat and avoid being eaten. These factors, along with finding mates and surviving abiotic stresses (such as extreme temperature, weather, and ultraviolet light) make up a large fraction of what we might call the ecology of an organism. Insects are no different: cope with the environment, eat, and don't be eaten. For insect herbivores, the food is decidedly vegetable, but what plant species to eat, what specific plant tissues to focus on, and having a sufficient supply, especially one that is not highly sought after by competitors, are important factors. Ditto for not being eaten. Insect herbivores may hide or avoid predators by crypsis (blending into the environment), or they may simply flee when they sense the risk of predation. However, some animals, like the monarch butterfly, eat in the open, do not blend in with their plant, and seem to advertise themselves through highly contrasting coloration. As we will see in later chapters, the coloration of monarchs is linked to their toxic diet. This is where the monarch-milkweed arms race took a turn, with monarchs taking advantage of milkweed's defensive poisons.FIGURE 2.4. Newspaper article about mimicry from the Washington Post, June 8, 1902.As early as the late nineteenth century, it was known that monarch butterflies were unpalatable, living with immunity from most predators, especially birds. A newspaper account from 1902 accurately describes not only their toxicity, but how bird predators learn to avoid the monarch's coloration and how the unrelated, and less toxic, viceroy butterfly benefits from coloration similar to that of monarchs (fig. 2.4). This phenomenon, termed Batesian mimicry, after the English naturalist Henry Walter Bates of the same era, will be discussed in chapter 6. What was less widely accepted at the time, but still studied among scientists today, is the origin of the butterfly's distastefulness.YOU MAKE ME PUKEIn the late nineteenth century, a Belgian scientist, Léo Errera, was studying plant poisons called alkaloids, widely known for their pharmacological effects. Caffeine, capsaicin, morphine, and nicotine are all alkaloids, to name a few. In 1887, he made conclusions about their functional role in plants: "Most alkaloid-containing plants are avoided by browsing animals. A few grams of alkaloids are equally efficient protective means as the most forceful thorns." But what if in the course of a coevolutionary arms race, specialized herbivores not only overcame this toxicity, but evolved a means to put these chemicals to work for themselves? This hypothesis is termed "sequestration" and suggests that at a late stage in the arms race, some herbivores might be taking in and storing toxic compounds from their host plants. Sequestration is at the intersection of "eat" and "avoid being eaten," because through the herbivore's leafy diet, a sequestered toxin is used to avoid being eaten by predators.If the plant produces toxins that are ultimately sequestered by herbivores for their own defense, then perhaps natural selection will favor reduced production of plant toxins. E. B. Poulton, a British evolutionary biologist, issued a call in 1914 for chemists to collaborate with biologists to solve the mystery of what makes monarch butterflies distasteful. Was it indeed the consumption of toxic substances from their milkweed host plants? And what are those substances? It took some sixty years to answer this question. Leading the charge was a group of talented scientists, including the Nobel Prize–winning Swiss chemist Tadeus Reichstein, the British naturalist Miriam Rothschild, and the young American lepidopterist Lincoln Brower. Not only did these scientists identify monarchs and milkweeds as one of the premier species pairs through which to study coevolution, but they also helped to establish chemical ecology as a discipline in its own right.The story begins with Dame Miriam Rothschild, a naturalist, one of the founders of the field of chemical ecology, and someone who had a knack for bringing people together. She was an eccentric force of nature, known for her love of fleas, her "delightfully disheveled garden," and her flamboyant purple dresses, typically coupled with a kerchief around her hair and high-top sneakers. She had no formal education, and yet she had a keen sense of the biology of organisms and for frontier questions in science. Rothschild had been studying parasites and butterflies, among other things, and had been interested in their toxicity and mimicry. In the early 1960s, she encouraged a graduate student at Oxford, John Parsons, to pursue the toxicity of insects feeding on milkweeds. Their choice of a toxic food and their advertisement with bright colors had suggested to Rothschild, as it had to naturalists before her, that sequestration (the accumulation of toxins from the host plant) was likely.Indeed, the toxic properties of milkweed were reminiscent of another plant, foxglove (Digitalis, from which the well-known drug takes its name), recognized to be emetic (vomit-inducing) for centuries. We now know that both milkweeds and foxglove contain compounds called cardenolides, and in the next chapter I will examine the essential chemical aspects of cardenolides in order to understand the milkweed-monarch arms race. Rothschild was interested in the hypothesis that similar chemical toxins in milkweed were finding their way into monarchs, making them distasteful and vomitous to bird predators. Although Parsons was not able to trace cardenolides moving from milkweeds to monarchs (could the monarchs be making them independently?), he did show the digitalis-like properties of several milkweed-feeding insects in a series of papers from 1963 to 1965. The last of these studies showed that monarch butterflies contained such a substance in the chrysalis and adults. Parsons purified the compounds and showed that they had toxic effects on frog hearts, guinea pig intestines, the blood pressure of cats, and enzymatic activity of human blood cells, and that they also caused starlings to vomit.Next enter Tadeus Reichstein, a Swiss steroid chemist, fascinated by both animals and plants. In 1950, he was awarded the Nobel Prize in physiology or medicine (with E. C. Kendall and P. S. Hench), for work that resulted in the discovery of cortisone, one of the most important stress hormones in animals. Only one year later, in 1951, he described cardenolides from close relatives of milkweeds (the same class of steroidal compounds that give Digitalis its kick). And a decade later, in 1964, Rothschild wrote a letter to Reichstein, requesting his assistance in isolating cardenolides from monarchs. At the time, there were no known steroids derived from insects, and accordingly this was a fateful challenge for the renowned chemist. Rothschild and Reichstein engaged in a collaboration that would last more than a decade, and their first preliminary results were reported by Rothschild at a conference in 1966.Lincoln Brower, a graduate student at Yale University, received his doctorate in 1957, working on the evolution of swallowtail butterflies. He quickly became obsessed with the hypothesis of mimicry among butterflies and the idea of sequestration, the notion that butterflies could accumulate toxic chemicals from host plants, thereby using these for their own benefit. In fact, his laboratory at Amherst College did much of the rearing for Parsons's, Reichstein's, and Rothschild's work, generating kilograms of monarchs (literally thousands of butterflies) for chemical analyses conducted in Europe. Not having access to the right equipment, and lacking abilities in chemistry himself, Brower and his colleagues took an unimaginably novel approach for their own studies of sequestration. Brower took thousands of monarch eggs and attempted to rear them on cabbage, which he assumed to be a benign host plant without toxins. If monarchs were gaining their toxicity from milkweeds, a cabbage-reared monarch would not be distasteful. His critical assay was not for the presence or absence of a chemical, but the behavior of a bird. In other words, Brower addressed the ecological consequences of the monarch's diet: would birds vomit if they ate monarch adults reared on milkweed (fig. 2.5), but not if they were reared on cabbage? He reasoned that if sequestration of plant poisons was important, birds would feed without nausea on cabbage-reared monarchs.The reason this approach seems unimaginable is that, in nature, monarchs eat only milkweed. Period. If you asked me, after studying monarch caterpillars for more than a decade, could I ever get them to eat cabbage, my answer would be a resounding no, and without a second thought. So, how did he do it? Over five butterfly generations, Brower reared monarch caterpillars bit by bit, only as long as they survived on cabbage. Hatched from thousands of eggs, nearly all the caterpillars were destined for a quick death by starvation, since they simply did not eat the unfamiliar food. In the first few generations, the larval survival rate was very low, with most of the caterpillars that did attempt to feed dying midway through development. Caterpillar death was not likely due to cabbage being deficient in some essential nutrient, but it could have been the result of cabbage's own defense compounds (mustard oils, or glucosinolates), or perhaps more likely because monarchs simply did not recognize cabbage as food. Whatever the case might have been, Brower persisted, switching them back to milkweed when they were near death. After this persistent set of rearings, in the fifth generation, Brower had nurtured a few caterpillars to adulthood that had fed only on cabbage and never on milkweed.FIGURE 2.5. Lincoln Brower's famous images of a blue jay barfing after feeding on a monarch butterfly. This highly repeatable assay of monarch toxicity usually concludes within twelve minutes.Working with wild-caught blue jays, and assaying their frequency of vomiting, he had an elegant experimental design. The birds were fed one of four foods: (1) monarch caterpillars reared on tropical milkweed (Asclepias curassavica), (2) monarch caterpillars reared on cabbage, (3) monarch caterpillars reared on a tropical milkweed vine called Gonolobus, or (4) mealworms, a most tasty food for birds. The milkweed-fed monarchs served as a positive control, scientific parlance for a treatment that should elicit an expected result: a barfing blue jay. Mealworms served as the negative control, since there was no expectation of vomiting. Brower's critical result was that cabbage-fed monarchs did not elicit vomiting. And furthermore, Gonolobus ended up being the exception that proved the rule. Brower had fully expected monarchs, which do feed on Gonolobus in nature, to be toxic when feeding on this milkweed vine. But, alas, the birds did not vomit. Much to his excitement, when Brower sent Gonolobus leaves to Reichstein in Switzerland, the results came back negative—no cardenolides. This was the confirmation that he needed to implicate plant toxins, which were now shown to be variable in host plants, as agents of the monarch's toxicity. Among Brower's four treatments, only when monarchs were fed a milkweed with cardenolides did they elicit a vomiting response from blue jays. The results were published in 1967.In 1968, Reichstein, Parsons, and Rothschild published a study that was the last important step in nailing down proof of the monarch's sequestration. In fact, monarchs had two concentrated cardenolides, calactin and calotropin, in their adult bodies, and these same cardenolides were found in their milkweed host. The authors reasoned, "The fact that the cardioactive toxin of the monarch butterfly is of the cardenolide type … supports the suggestion that it is derived from the food plant and stored either unchanged or with only minor metabolic transformation." This paper, building on the three previous studies, sealed the deal on the paradigm of sequestration.Later on, as the sequestration paradigm was cemented, some tension occasionally arose between Rothschild and Brower. They continued to work independently on monarchs and their sequestered toxins for decades, and perhaps both worried about their respective legacies. Who would be remembered as the discoverer of monarch sequestration? A few points about this scientific tension are worth explaining. First, it was Parsons and Reichstein (not Rothschild or Brower) who did the early heavy lifting in terms of physiology and chemistry, inspired and aided by Rothschild and Brower. They could not have done this work themselves. Second, Rothschild and Brower were themselves collaborative and reciprocally inspiring. In each of their respective early publications, the acknowledgments section is very telling. In most scientific publications, acknowledgments are provided at the end—usually crediting colleagues who contributed substantially and generously, but not enough to warrant being a coauthor of the study. The spirit of the acknowledgments in these four key studies is one of excitement, collaboration, and sharing. Letters, live butterflies, dried leaves, ideas, and inspiring words were being shipped across countries and oceans, with nearly all names appearing in all four papers' bylines or acknowledgments. That is what made this science move forward and, more generally, what makes science great fun. Despite the tension between them in later years, Rothschild and Brower share the legacy of being pioneers of chemical ecology and hugely important in the development of knowledge about monarchs and milkweeds.

What people say about this book

Art Shapiro, “What we know about Monarchs that is and ain't so. I'll own up to a prejudice. I knew Anurag as a grad student, and he collaborated with my then-student Jim Fordyce on research. Jim and Anurag were the two top students in their cohort here at U.C. Davis and both were clearly destined for great things. I was happy as the proverbial clam when Anurag was hired in my old home Department at Cornell and have followed his career with great interest. This book, as expected, is a tour de force. But I want to dwell on one aspect of it in this review; you'll soon see why.The Monarch has become a "poster child" for conservation. It's "charismatic;" people love it. A dull gray-brown dung beetle with identical conservation status would never be adopted as a fund-raising icon like the Monarch has been. But as the 19th-Century humorist Artemus Ward warned us, what we don't know don't hurt us as much as what we know that ain't so. If you've been reading the mass media, including the "New York Times" and my own local sheet, "The Sacramento Bee," you "know" that the Monarch is in existential trouble because there isn't enough milkweed left for its caterpillars to eat. That, in turn, is due to the promiscuous use of agricultural herbicides, enabled by the spread of genetically-engineered "Roundup-Ready" crops. The solution is to invest massively in planting milkweed to "save the Monarch"--one recent article advocated a multimillion-dollar investment in the effort. To which I say "Poppycock!"Our research group was the first to document Monarch declines in California, where there is no milkweed shortage. The declines here (which were temporarily reversed during the recent drought, for unknown reasons) were more severe than in the East and Midwest, where all the to-do is concentrated. The case for a milkweed shortage anywhere is very poorly documented and much weaker than the propaganda would have you believe. Because my research is not Monarch-centered -- we published first on the California decline only because we had a unique long-term data set which was gathered for a much wider (not Monarch-focused) investigation -- I do not have the professional bona fides to challenge the milkweed-limitation hypothesis (which is all it is). But Anurag does. And he does. Read his Chapter 9. And then, applying the "cui bono?" ("who benefits?") test, ask yourself why you are being fed this spurious argument that milkweed is the critical issue. Monarch studies have long been fraught with politics and personal and professional rivalries (some of which come up in this book). Before we go investing massively in a project unlikely to have any effect--especially when dollars for conservation of anything are increasingly scarce and intensely competed-for -- we should know there is another side of the story than what we read in the op-ed pages of the "Times." Read this book! Pass it on!”

Aya Katz, “A Lyrical Scientific Exploration of the Relationship of Monarchs to Milkweed. Anurag Agrawal's Monarchs and Milkweed is not the first book that I have read about the monarch butterfly. The first one arrived in the spring of 1967 as part of the Weekly Reader book club, and it was called The Travels of Monarch X . I was learning English by total immersion in a first grade class in Romeoville, Illinois and was not that impressed by the story of Monarch X at the time. It was not until I read Agrawal's book fifty years later that I understood the significance of the earlier volume.Anurag Agrawal's book is easy to read, has a poetic rhythm to it, and yet it is a book about science. It describes the facts of the monarch butterfly's life, as we currently know them, and it also relates amusing moments from the lives of those studying the monarch's life cycle and migration patterns. Did you know that monarchs are not pollinators, even though they have that reputation? Did you know that they add nothing to the lives of the milkweed plant that regards them as a pest and tries to poison them? That most monarchs live for less than eight weeks, except for the virginal autumn migrators, who, if they survive could live for as long as eight months? Or that Dr. Fred Urquhart, at whose behest the book about Monarch X was written in order to recruit children for a monarch tagging venture, was sharing the location of the overwintering ground with National Geographic when it was found in 1975, but wanted to keep it hidden forever from his colleague Dr. Lincoln Brower? Did you know that even though population studies indicate that the Monarch migration to Mexico is endangered, the monarch butterfly species itself is not endangered at all?All this and more can be found in Monarchs and Milkweed. I highly recommend it. A longer version of this review can be found on PubWages dot com.

The Travels of Monarch X”

Gregory J. Auger, “Written by a renowned scientist who has studied this beautiful organism for years. If you are an appassionato of the fabled Monarch butterfly, or even of butterflies in general, you won't want to pass up this book. Written by a renowned scientist who has studied this beautiful organism for years, it's a clearly written and up-to-date account of what we know and what we don't know about this mysterious beauty. Monarch caterpillars are destined by evolution to eat only milkweed plants -- yet those same milkweed plants are poisonous to the caterpillars. They have no choice in the matter. Once you get over the emotional pathos of this coupling -- what you require to survive will most likely kill you -- you'll be hooked on reading about the seemingly endless strategies that the caterpillars have evolved in order to survive their ordeal. Who knew that caterpillars would have to face such grueling tests of their ability to persevere?The book is written so as to be friendly to the lay reader and is extremely well-illustrated. If you are looking for authoritative texts on the basic biology of these lightweight, ephemeral beings that fly all thousands of miles to a special place in Mexico where they can safely winter, this is a book you will want to own. Thanks to the scientist for taking the time to write it.”

Herman, “A detailed reference about the Monarch butterfly.. This is a great reference book to learn all about the biology, evolution and migration of the Monarch butterfly, and its relationship with the milkweeds. The book is well-illustrated with photographs, drawings and charts, and provides clear, detailed information. It's great for naturalists who want to learn much more than what you can find in most field guides.”

Alok, “Loved it. Loved it”

The book by Anurag Agrawal has a rating of 5 out of 4.7. 163 people have provided feedback.

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