Monarch of the Butterflies describes in detail the life story of this, one of the best-known and most-loved of nature's creatures. In it the author introduces us to what we've learned from and about the monarch, through science, literature and art.

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MONARCH OF THE BUTTERFLIES

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Life History

"There's nothing constant in the world,
All ebb and flow, and every shape that's born
Bears in its womb the seeds of change."

- Ovid

There are many ways to know the world: through poetry, and art; spiritual inspiration; intuition; logic and reason. And there is science. As a scientist, though I write poetry and enjoy art, use my intuition and try to be reasonable, I am especially fond of what is loosely called “the scientific method.” It may not be the most impressive or emotionally resonant way of knowing the world, but in the long run it is the most trustworthy.

As a teacher, I tell my students: Scientists let the world tell them how it works. That’s not an easy thing to do, as it turns out. We have our preconceptions, our faulty perceptions, our misconceptions. The road from ignorance to understanding is not a throughway; more like a winding rustic road, full of wrong-turns and detours, some of them offering beautiful vistas, seductive but unreliable. For centuries now we have bent over microscopes, shivered at chilly telescopes, sampled soils on the edges of simmering volcanoes, babied dangerous distillations or wrestled with rebellious DNA gels. As Steven Jay Gould[1] put it: “Most daily activity in science can only be described as tedious and boring, not to mention expensive and frustrating.” But the hard work, coupled with the insights of pioneers in every field, funded to a large degree by your tax money, have set at our feet one wonderful gift after another. One by one we can pick up pieces of the world never before seen and with them put together new patterns and new understandings of how it all works. And each new vista brings with it the promise of more to come.

The growth of scientific information has been described as exponential. It is that and more. It was barely a hundred years ago that August Weisman suggested that genes were on chromosomes. Dr. Hugh Iltis related to me and other students in his evolution class at the University of Wisconsin how his father was a friend of Weisman’s. We are but two generations from even knowing where the genes are, and now we redesign them. Einstein's three seminal papers were all published just over a century ago. Yet how far we've come since in our understanding of the universe, its beginning and its evolution.

While there are just over 700 species of birds nesting in the U.S. and Canada, there are about 90,000 species of insects already identified, and plenty yet to be named. Some say that insects count for about 70% of all animal species on earth. We know quite a bit about some of them – especially the ones we call pests. But the behavior of most, their ecological interactions with each other, the plants they feed on or pollinate, and the predators which eat them, remain to a large degree behind the veil. Those who feel uncomfortable without the resonance of a mystery lurking over the hill may find that satisfying. It means too there'll never be a shortage of good questions to answer, each a potential career. But it also means we're still on a steep learning curve about the world we inhabit.

In biology the study of an organism's birth, development, and death is called its "life history." It turns out we know quite a lot about the life history of the monarch.

All life histories have something interesting about them. But our monarchs give us something special: these hunky caterpillars who transform themselves into delicate butterflies, ugly ducklings who crawl off to sleep only to wake one morning as lovely swans into a completely new world. Within the hemispheres of our brain resides a terrible knowledge. On the one hand we cling desperately to our self-being but on the other know only too well of our constant becoming. We are who we are, yet we constantly become something else. We cling to the hope that our transformations, so often out of our control, will be for the better. The monarch's throwing off the cloak of the ever-hungry larva, tied by its desires to the mundane world and emerging as a light, free and beautiful butterfly is emblematic of that hope, that our own transformations, the little daily ones and the big ones—birth, romance or marriage, and finally death— will be for the better.

But the process of metamorphosis resonates with us for even deeper reasons than this, which I believe have to do with the very fundament of who we are, who we think we are, and how we perceive the world.

Consider a tree: any tree. The tree you see is not the tree as it is. It is both much more and much less. It is more because we perceive only its surface. We see its bark, the lichens it supports, the filigree of its leaves and in spring or summer its dangling flowers. But we cannot see the practiced orchestra working feverishly away inside it – its enzymes, chloroplasts, intercellular junctions, xylem and phloem, a complexity ultimately beyond our ken. And the veil is even more opaque than that: that tree's DNA, almost certainly like each of ours absolutely and forever unique; its own particular history from seed to sapling, the winds which bent it and rains which watered it, or hailstones which threaded the leaves off it that summer not so long ago; the ancient evolutionary history of its clan, of which it is only a momentary epiphany. Each tree is an infinity we cannot plumb.

But the tree is at the same time less than what we see. Because by knowing of trees, the cottonwoods we've camped under on the high plains, or the western cedars and Douglas firs of the Olympic rainforest; and of wood floors, which welcomed us into the old hardware store of our childhood, or of Birnhamwood moving to Dunsinane which brings to our every meeting of a tree the cold winds shrieking about the thanes of Cawdor; and the squirrels, gray or black or red, chattering and nesting in its crown, which we have encountered in parks in Europe or on the college campus we came to as wide-eyed freshmen; and of the memory of the sweetness of maple syrup as our mother poured it over the steaming Sunday-morning pancakes; with all these, which are uniquely our own and not of the tree itself, we make the tree more than it is.

The poet Wallace Stevens wrote that Marianne Moore had "the faculty of digesting the 'hard yron' of appearance." So with our eyes or ears or nose we ingest the tree, and with our imaginations we digest it. And in digesting it we make it part of ourselves, and in doing so change not only ourselves, but the tree, too, transmuting and transforming it's image while it transforms us.

It's said that though his medium was poetry, Stevens' heart was the heart of a painter. His poems in many ways are about the transformation of the visual into something uniquely and very human. Of painters, I think none is closer to Stevens than Van Gogh. By transforming the everyday world — the peasants sitting down to a meal of potatoes, a pair of old boots, a grain-field with crows – he shows us something we didn't know before about that world, and something new about ourselves, too. Most importantly perhaps Van Gogh's and Steven's imagination reflect to us an image of the vitality at the center of life, which intimacy with nature can also bring us into intercourse with.

Each day for each of us the world offers itself to this substantial transformation. It is the ground we walk on, the stuff with which we make our art, create our gods, and ultimately ourselves by ourselves and in relation to others.

Our word imagination comes from the Latin *imago*, meaning a picture or representation. The Swedish biologist Linneaus applied the term to the adult stage of insects which undergo metamorphosis – so the butterfly is an imago. As we'll later see, certain tissues in the larva are called imaginal discs, because they carry in them a genetic representation of the adult.

Stevens is the great poet of the imagination. With the will of our imagination, he says, we can actively participate in these daily metamorphoses, and in so doing become more than we are; we can achieve a meaning-full relationship with the world. In *The Figure of Youth as a Virile Poet* he says "We say that poetry is metamorphosis…" His poem *Final Soliloquy of the Interior Paramour* is nothing less than a love-ballad to the imagination.

"We say God and the imagination are one.
How high that highest candle lights the dark."

and in Notes *Toward a Supreme Fiction* he says that:

"the freshness of transformation
is the freshness of a world."

Poets are naturally drawn to butterflies. There's a photograph of Walt Whitman holding out his hand, on which a butterfly has alighted – though it's been pointed out that this is most likely a bit of self-promotion by Whitman, the supposed butterfly being no more than a cardboard cut-out.[2] I know of no poet who wrote more of butterflies than Emily Dickinson. She speaks of the butterfly emerging from its chrysalis and putting on its "assumption-gown." Here is her version of the Catholic's Sign of the Cross: "In the name of the bee, and the butterfly, and the breeze, amen." Though a recluse, as though cloistered within her own chrysalis, each day she unfolded the wings of her imagination which became her own "assumption-gown."

Metamorphosis and change are woven into the very fabric of our lives. But necessary as it is, change can be hard. So it seemed apt that in the highlands of Mexico, near the foot of one of the monarch's over-wintering sites, in Valle de Bravo's church of Saint Francis of Assisi – patron saint of nature – I came across the image of *La Senora de Sagrada Grazzio, abogado de las causas dificiles y desparadas*. Our Lady of Divine Succor, intercessor in difficult and desperate causes. As I turned to leave the church I encountered a pair of women, who like so many of Mexico's poor, live rich full lives surrounded by constant and what would be to many of us insurmountable difficulties, on their knees in slow migration toward the altar.

So yes, our little half-gram butterfly not only navigates the treacherous waters of metamorphosis, it then has the gall to attempt a long flight to a mountain enclave it's never visited, there to take on, unprotected from the elements, five months of hard winter. Much more about that, later.

It's no accident that reproduction is fun. Any species which didn't reproduce, no longer is. In the animal kingdom, it's the story of sperm heading off to meet egg, and it's seldom a straight-line narrative. Like us, monarchs start their lives as one cell, the fertilized egg called a zygote. Unlike us, butterflies have hundreds of brothers and sisters, all with the same mother but who knows how many fathers. We will learn more about that – the female monarch's innate polyandry—in another chapter.

An egg is DNA wrapped in a fancy package. Yo' momma's DNA plus yo' poppa's DNA equals…..you! Monarch or not-the-monarch, alike. Like every one of us, because they are sexually reproduced, except for the rare identical twin, every person and every monarch is genetically unique, and in the long history of the universe never has been and never will again inhabit the earth.

Pliny the Elder writes about nearly everything in his encyclopedic *Natural History*. According to him (Book 6, chapter 37), lepidopteran eggs are distilled from the morning dew by the heat of the sun. It is a lovely description, even if not scientifically correct. It does suggest, however, that in his time – the first century C.E. – readers expected not just descriptions but explanations for natural phenomena. Perhaps that is a trait which makes us uniquely human — not just seeing but needing to explain. One wonders if a chickadee carries that burden, wondering where from come the sunflower seeds on the feeder?

Lepidopteran eggs come in many shapes and sizes. Monarch eggs are elongated – prolate — spheres. Technically, they are referred to as oblate spheroids. They stand upright, about the size of the head of a pin and milky-white in color. You'll find them on the underside of milkweed leaves. Under a microscope you can see that the shell of the egg has one or more tiny holes in it called micropyles through which the sperm entered. The embryo inside the egg is alive, and needs oxygen, so the micropyle also serves as an opening through which the embryo breathes. In addition to its DNA, the egg contains yolk, which holds the nutrients for the growing embryo. Because monarchs are poikilotherms, whose body temperatures closely track that of the ambient air, and metabolic reactions are temperature-dependent, (again, much more about this later) development inside the monarch egg goes faster or slower depending on the temperature. So it can take from perhaps four to twenty days for the embryo inside the egg to mature, often four to seven. As the cells within the egg divide and the embryo begins to develop, special homeotic genes control the formation of the embryo. These genes are very similar to those which early on in your own development set down the pattern for you: head, chest, arms and legs.

The development from a zygote to the tiny, first-instar larva which chews its way out of the egg is itself a near-miraculous choreography of genes turning on and off, proteins dancing their way across the stage and out, with a continual chorus of metabolic reactions, all leading towards the finale of this act: the transformation from egg to larva.

According to the philosopher David Hume, "There is no quality in human nature which causes more fatal errors in our conduct, than that which leads us to prefer whatever is present to the distant and remote." Gifted with hindsight and foresight, our challenge is to immerse ourselves in the here and now without getting stuck in it. But the distant and remote, to a tiny first-instar monarch larva, just out of its egg, is of no interest at all. To achieve its destiny, still hidden over the close horizons of the milkweed leaf, it simply hunkers down and eats, eats, eats. It's a simple life, really. No bills to pay, kids to ferry to soccer practice, tests to take or bosses to satisfy. Just eat, eat, eat. And it does that with a Zen-like single-mindedness.

Its DNA directs the larva to eat. It's a job for which its DNA has well-equipped it. Its mandibles are hard and rimmed with teeth-like structures; near the front, shaped more like incisors, and in the back more like molars. With these and the muscles attached to the mandibles, it bites off and chews up chunks of the milkweed leaf. It uses its maxillae and the palps to direct the food towards its mouth. There, special sensory cells tell it what the food smells and tastes like, and if the food's chewed well enough to swallow.

The monarch larva's tubercles – antennae-like structures — are carefully tuned, by natural selection, to pick up and respond to only certain signals. Especially, but not only, the smells given off by a nice young milkweed leaf. Our senses are tuned, too – we only perceive a small part of the visual and auditory spectra which are all around us. Our sense of smell is miniscule compared to that of our best, canine friends. It's hard to say what the olfactory world of a monarch caterpillar is like. Further research into their sensory and neural biology may someday allow us to paint a better picture of it.

Monarch larvae, born as they are on the plant they will be eating, don't need to look for their food. But they do have eyes, with simple lenses, that allow them to form a rough though poorly-resolved image of the world, an image which at least helps them to see the approach of potential predators and if necessary fall off the plant to escape.

Some of you have had the "pleasure" of giving birth. Mothers are more likely to remember their childrens' birth-weights than their own. Perhaps you do know your own birth-weight. The US average is about seven and a half pounds – less than six, if you're a twin. The first-instar monarch larva crawls out of its egg at an average birth-weight of slightly less than half a milligram. That's not much. If you weighed the US average on birth, it would have taken somewhere around 9 million of the newborn monarch larvae to balance the birth-weight scales. Depending again on temperature, and the nutritional quality of the leaves it munches, munches, munches, over the next week or two the larva will end up weighing nearly a gram. Measured as a ratio, by the time it's done being a larva and ready to crawl into its chrysalis, it will weigh almost three thousand times what it weighed at birth.

Okay. Let's do the math. Let's say you were an average infant at birth. That would make you as an adult, well, twenty thousand pounds. Ten tons. Careful where you step! I don't think those stairs, or that floor, will hold you. And better get a truck to haul you to school or work. A big one.

The very first meal an infant monarch enjoys is the shell it crawled out of— a nice high-protein snack. (You can watch a video of this, and many other interesting monarch clips, by searching on *YouTube* for "monarch butterfly.") The tiny larva, barely visible at this stage, often spins a silk pad to attach itself to, so it doesn't fall off the leaf.[3] But the moment it turns its attention to the big, green tabletop it was born on, it becomes an eating machine. Having worked on a dairy farm, and also having raised many monarch larvae, my imagination connected the dots between these chubby chewers munching milkweed and the bigger, four-legged Holsteins I once kept bulked up with hay and silage. Eating and pooping seem to be what both are best at. Cow-poop we call manure. Insect poop is called *frass*, and from measurements done in my ecology classes we determined that for every milligram of weight gain, monarch larvae deposit about two milligrams of frass. Those of you who've raised larvae have likely been astonished, as I was, at how rapidly it can build up.

The monarch larva's food pyramid is not strong on menu choice. To meet its daily requirement of water (for it never drinks) it eats umpteen servings of milkweed leaf. For calories, it needs plenty of milkweed leaf. Nutrients such as proteins, required fats and minerals it gets by eating a few more servings of milkweed leaves. Finally, to ingest nasty-flavored chemicals which protect it from potential predators, it grazes on…milkweed leaves. The term *pharmacophagy* has been applied to animals eating not for basic nutritional needs such as calories or protein, but for the chemicals in the food, needed for various purposes. Most animals select the days' menu not only based on what's available, but what they feel they need. There are reliable reports of deer standing in creeks to eat fish – nature's nutritional supplements. And monarch larvae will sometimes turn up their noses at milkweed. One woman who raises monarchs put a slice of watermelon in with her caterpillars and they quickly left the milkweed and turned to munching its rind – though they may not have been able to properly develop on such a sweet dessert.[4] Final instars also seem to like butternut squash.[5] Experience in raising larvae suggests earliest-instar larvae seem to prefer the particular species of milkweed they first taste, though later instars are more adventurous in their selection of food.[6] Clearly more remains to be learned about what they will and will not accept as food, and the nutritional and growth consequences of these foods.

Mathavan and Muthukrishnan[7] studied a close relative of our monarch, the queen butterfly *Danaus chrysippus*. By reducing how much they were allowed to eat larval development was stretched out from 6 to 18 days. While the pupae produced by the underfed larvae did not take any longer to eclose (hatch out as adults) they were smaller than normal. My ecology students made similar observations, and we also noted the smaller adults these smaller pupae produced.

It's a story we learn as children, how the monarch caterpillar sequesters chemicals found in the bitter milkweed juices to protect it from becoming someone's snack. But that is just the synopsis. Nature has built a complex plot-line, almost poetic in its details, which deserves closer study.

Female monarchs lay their eggs on milkweed plants, whose scientific name is *Asclepias.* Like many plants, milkweed is a chemical factory, producing what are called secondary metabolites to protect themselves from being eaten. We humans make use of these chemicals – nicotine from tobacco, cocaine from the coca plant, caffeine from coffee are only a few examples. Milkweed itself was used by native Americans. The Chippewa (Anishanabwe) of the northern Midwest gave it to lactating women to stimulate lactation – perhaps on the same principle of resemblance which made the mandrake plant magical to medieval Europeans. Roots from milkweed were mixed by the Anishanabwe with roots of boneset and applied as a charm on whistles, to call deer.[8] Other tribes used the root as a laxative and diuretic, and the milky latex for curing warts, moles and ringworm. Mohawks apparently combined it with an extract of jack-in-the- pulpit as a contraceptive – perhaps actually as abortificents, because both contain dangerous toxins.[9]

In food-preference trials, Vickerman and de Boer[10] showed that monarch larvae prefer species of *Asclepias* to other plants. Extracts of milkweed leaves, but not other potential foods, stimulated the larvae to eat, so the leaves must contain some kind of chemicals – as yet unidentified – which act as phagostimulants, the larval equivalent of walking by a bakery.

The toxic glycosides (also called cardenolides) are about forty times more concentrated in the bitter white latex of the milkweed plants than in the leaves themselves. Monarch larvae have been seen, especially in early instars, to cut a partial circle in the leaf they are feeding on, which causes the more toxic and/or sticky latex to drain. Older larvae sometimes cut the petiole which holds the milkweed leaf to the stem, which also decreases toxins.[11] Because the leaf bleeds out its toxins at the cut, while eating the cut leaf the insect is exposed to as little as 10% of the toxins.

But as it so busily eats, the monarch larva is stepping farther and farther out onto thin ice. Depending on the concentration of toxins in the particular plant it munches, it is in fact poisoning itself, and some number of those happy newborns do just that. Not all milkweed species, or even plants of a particular species, have the same concentration of toxins. Zalucki, Brower and Alonso[12] manipulated latex concentrations in milkweed leaves by tweaking them with forceps, which causes the latex to leak and the total concentration of glycosides in the surrounding tissues to go down. They found that larvae that fed on the damaged leaves, with less glycoside, grew about twice as fast as those which fed on undamaged leaves. Some of the larvae became stuck to the latex, and died. Early instar larvae are especially sensitive to the latex. The latex is sticky, and hard to clean from their mouths and heads. Videos showed some, who'd consumed the high-toxin latex on undamaged leaves, becoming cataleptic and falling off the leaves. In similar experiments, first instar larvae grew faster, and experienced lower mortality, when the glycoside concentration of the leaves was reduced by artificially causing the latex to leak from the leaf.[13]

So the larvae, though protected by the glycosides, pay a price — like medieval knights donning heavy armor. By overloading their own detoxifying systems with high-titer milkweed, they can either stunt their growth or in some cases kill themselves. It's not a free lunch!

Individual monarch larvae hatch onto a particular milkweed plant which can have low, medium or high concentrations of cardenolides. One study found the average concentration to be about 50 micrograms of cardenolide per 0.1 gram of common milkweed (*Asclepias syriaca*) dry tissue. Variation among plants however was very wide, from 5 to 229 microgram per 0.1 gram. On average the 158 larvae assayed had a mean of 234 microgram per 0.1 g of larval tissue. In other words on average they concentrated the cardenolides in their bodies by a factor of about 4.7 times. Eastern plants and larvae had higher concentrations than more western. Milkweeds in small patches had more cardenolides than those in larger patches, though the larvae did not. Younger plants, and those in the sun had higher concentrations of cardenolides, as did the larvae found on them. One cardenolide called aspecdioside was found in 99% of the plants and 100% of the larvae. Another, desglucosyrioside, was not found in any of the plants but did occur in 70% of the larvae, who must therefore be capable of synthesizing it themselves, perhaps from other cardenolide precursors.[14] Other studies showed that larvae who eat leaves with high concentrations of cardenolides no longer concentrate it. Instead, they reach a kind of saturation level within their bodies, above which it becomes toxic to them.[15]

That's the thin ice. You have to eat to grow, and like most salads milkweed leaves are low in nitrogen. So you have to eat enough to grow and to meet your nitrogen and other nutritional requirements, but not so much as to poison yourself. Studies show that when the milkweed plants are grown in limited nitrogen, the larvae have to eat more. But you also eat to protect yourself from predators, by sequestering the toxins in your food. Consume too much toxin and you're sick or dead. Consume too little and you either starve, don't get enough nitrogen to grow, or don't have enough toxin to protect yourself should a passing bluebird swoop down to try you out. It's a fine line you walk to get it just right. Some do, some don't. Time again to call on *Our Lady of Difficult and Desperate Causes.*

Of course if every one of the hundred or more eggs a reproductive female laid survived, the world would soon be overrun by monarchs. Most of course do not survive. Zalucki and Brower[16] studied survival of monarch larvae in north-central Florida on the sandhill milkweed (*Asclepias humistrata*). Survival of first- instar individuals in the wild ranged from about 4% to 12%. That's not mortality, that's survivorship! About a third of the larvae were found glued to the leaves by the plant's latex. Some starved because their mandibles were glued together as the latex dried. Survival of eggs collected in the field and hand-raised was much higher. Of 219 eggs collected and hand-raised, 62% hatched into caterpillars, and 64% of eggs hatching into caterpillars were released as adult butterflies.[17] Similar results for survival and longevity have been found for many hand-raised or zoo-kept animals, protected from natural predators and other sources of mortality.

In nature some larvae just fall off the leaf during a storm. Or a newborn larva, just finishing its eggshell snack, might bite down onto a leaf's vein, with its high-titer toxin, and go into a seizure, unable to move or hide from predators.

Evolution naturally has been busy designing predators of the larvae. The monarch larvae monitoring project[18] has shown that various parasitoids, including tachinid fly larvae, also contribute significantly to larval mortality. More on them, and other factors which increase larval mortality, in a later chapter.

For the moment let's focus a molecular microscope on the chemicals the larva is eating and sequestering. They are a mix, a cocktail of sorts. Milkweed's genus name *Asclepias* comes from the Greek god of medicine. Like the Native Americans, Europeans have made use of milkweed chemicals. The term cardenolide comes from their use in treating congestive heart failure, because they increase the contraction of the heart.

These cardiac glycosides are found in a variety of plants, including the foxglove *Digitalis lantana*, from which we get the powerful cardio-stimulant digitalis. Though not found in milkweed, ouabain is a related compound whose toxic effects have been studied as a model of other, less common cardenolides. How is it that monarchs munch cardenolides with relative ease, while other herbivores who might ingest it become so rapidly sick? Modern molecular biology provides us an answer.

Ouabain is toxic to most animals because it inhibits a very important enzyme called ATPase – a protein which helps break down ATP (adenosine triphosphate) and in doing so releasing energy. If we can't break down ATP, we run out of energy – it's like having a laptop with its AC-adaptor but no place to plug it in. Eventually, the cells' batteries run dead.

So if you could evolve an ATPase which was not sensitive to oubain, you could build up higher concentrations of it and stay alive, while at the same time becoming toxic to predators. That's exactly what monarchs have done. Ouabain (and presumably the many related cardiac glycosides in milkweed) binds to the ATPase to make it inactive. But monarchs carry a mutated form of the ATPase. At position 122 of the protein, compared to most lepidopterans, monarchs have an abnormal amino acid – a substitution of the amino acid histidine for an asparagine, which causes the ouabain not to bind to, and inhibit, the ATPase.[19] These same scientists went on to clone the binding-site on the ATPase to which ouabain binds, and put it into human kidney cells. These cells were much less sensitive to ouabain than normal kidney cells. The leaf beetle *Chrysochus*, which also sequesters cardenolides, has the same amino acid change, from asparagine to histidine, at position 122 of its ATPase.[20]

Remember that our larva is busy munching milkweed for its nutrients as well as its glycosides. We don't normally see or think in these terms — because I suppose evolutionarily it would have been too distracting — but in a field scattered with milkweeds, each plant is not only genetically distinct but because it has grown in a local microenvironment, nurture has contributed to its uniqueness. This means that each milkweed has more or less glycosides, and each is overall more or less nutritional to the individual larva, too small to migrate off the plant it was born on to find a better selection at nature's salad bar. Milkweeds can respond to being eaten by dialing up their production of toxins. This ability, called an induced response, is quite common in plants. But depending on its genetics, each plant is more or less able to increase its load of toxins when it finds itself being munched on. If the particular milkweed which is the larva's birthright is low on nitrogen, it must eat more to meet its own protein requirements.[21] But if it eats more, it gets more toxins; so let us hope for the larva's sake that the low-nitrogen plant it's munching is also low on glycosides, and not too swift at dialing them up.

We'll step off the glycoside treadmill in just a moment. One further question though. What happens to the poisons our larva is ingesting? By feeding larvae milkweed leaves, then assaying them for cardiac glycosides, Frick and Wink[22] showed that within two days after ingesting them the toxins wind up in the integument (skin). The midgut tissues and the hemolymph (insect equivalent of blood) on the other hand seem to function merely as transient compartments for them – shopping bags for bringing the groceries home. They also found that a little over 60% of the glycosides were transferred from larvae into the butterflies during metamorphosis, the main sites of storage in the butterflies being the wings and integument.

It may be that not all the poisons a particular monarch larva lugs around with it come from the milkweed plant. Two subspecies of the monarch found in South America are capable of synthesizing some cardioactive toxins even if they've been fed a diet which does not contain them.[23] Evidence mentioned above regarding the glycoside desglucosyrioside suggests North American monarchs make some of their own toxins.

Most species of butterfly larvae, of course, do not feed on toxic milkweed. Bernd Heinrich[24], a wide-ranging biologist who has written much about insects and whose book *The Mind of the Raven* is a revelation of complex corvid behavior, observed that palatable species of caterpillars – those not protected by toxins — tend to always feed on the underside of leaves, nap during the day while feeding at night, and after snacking on a leaf tend to crawl and hide themselves relatively far from the leftovers which might signal a predator of their whereabouts. Less palatable species of caterpillars often don't do this. In other words, palatable species have evolved behaviors which unpalatable species have not had to evolve — or it may be that unpalatable species like the monarch have over time lost those protective behaviors.

Another strategy for survival of palatable larvae is camouflage. Because they are so busy eating out in the open and don't have time or means to defend themselves, many moth and butterfly larvae have evolved creative ways of camouflaging themselves. Some you could easily mistake for pine needles. They even sit that way on the twig, straight-backed as Amish children in a classroom. Others almost exactly resemble a wet glob of bird poop. Yet others look like broken twigs hanging off a branch. Sometimes instead of camouflage they are masters of disguise. The head of one (*Hemeroplanes*) is a perfect image of a minute snake. Another looks like a snail. When threatened, *Cerula vinula* turns its equally comical and frightening red face at you. Many have sharp and sometimes toxic spines.

But our *Danaus* larva isn't camouflaged, is spineless and doesn't resemble anything other than itself, a very brightly-painted fat and tasty caterpillar. It uses its toxins to protect itself; and it uses its bright colors to advertise that it is poisonous. Its broad, bright bands of yellow, white and black are called by biologists aposematic coloration. Such bright colors are also worn by poisonous snakes like the coral snake, by the gila monster, and by many poisonous spiders with bright yellow or red markings. Aposematic coloration simply says: Stay away!

The adult monarch's toxic qualities have led other species, such as the adult viceroy butterfly, to mimic it. You'd think the same strategy would work for other species of larvae, too, but there are only a few known examples of larval mimics of unpalatable larvae. The black swallowtail larva mimics the monarch larva, but is itself unpalatable. The clouded crimson mimics both. The pipevine swallowtail, which like the monarch sequesters toxins, appears to be mimicked by the great spangled fritillary. Female pipevines appear to be born with more toxins than males. Over their lifetime they seem to lose these chemical defenses, perhaps by depositing some in the eggs they lay. Older female pipevines, low in chemical defenses, are in a sense mimics of more poisonous adult males. [25]

Not all monarch larvae are identically colored; again, nurture plays its tune on DNA's keyboard. Monarch larvae raised at cooler temperatures have more black and less white and yellow pigment than those raised at warmer temperatures, probably to increase solar heat gain on chilly mornings.[26] In a similar way in some species of butterflies adults born in cooler springtime are darker than those born during high summer.

We'll look more closely at the complex co-evolutionary interplay between the monarch and the milkweed in the *Ecology* chapter of this book.

Time now, though, to pay the piper. Dr. Miriam Rothschild was one of the first biologists to study the relationship between the monarch's sequestered chemicals and the aversion predators have to them. Her uncle Walter Rothschild possessed what was likely the world's largest collection of butterflies and moths, some two million specimens. Miriam was a prolific letter-writer, composing a letter every day for 35 years to her cousin, head of the Rothschild bank in Europe – to him alone, more than 13,000 letters. During World War Two the Rothschild estate she lived at housed American airmen, including for a time the already-famous Clark Gable.

Miriam Rothschild had little formal training in biology. She believed in studying nature, not books. She once said "The types of tests devised by the appropriate authorities in Britain today assess the size of the child's bottom, rather than that of its head." She became an expert on the reproduction and taxonomy of fleas, having mounted at least 60,000 of them on microscope slides. Unable to breed them in a laboratory, after discovering that the female flea's reproductive cycle was synchronized with that of the rabbit doe, she was able to breed them like…rabbits.

She is considered by many to be the founder of the study of chemical ecology. Her work on pyrazines, often found in toxic prey such as our monarch larvae, showed that the unique odor of pyrazines actually helps improve an animal's memories – a good thing to do if you want to impress someone who's just gotten sick to not eat you or your kind again.

Dame Rothschild published more than 275 scientific papers, and was awarded honorary doctorates from Oxford and Cambridge. She was well into her sixties when an eye disease prevented her from continuing her work on fleas. So she returned to her earlier interest in butterflies, which she described as "Dream flowers, childhood dreams which have broken loose from their stalks and escaped into the sunshine. Air and angels!"

In her eighties she campaigned with Prince Charles for replanting England's wild places into wildflower havens for butterflies, and under her influence Highgrove, one of the Prince's properties, became one of the first to feature not expanses of lawn along its drives but swaths of wildflowers. When asked among all her life's accomplishments what gave her most joy in her life, she answered having a family.

This is from one of her letters, written on Christmas Day, 1989, when she was 82:

> "I am playing about with wildflower promotion, a bit of propaganda on television, a book trying to combine poetry, painting and natural history, a film with David Attenborough, a few vague experiments with quails and pyrazines, but really doddering along, falling over and rather surprised and glad to still be around. I can occasionally look down the microscope but pay heavily for it afterwards with a smashing headache. What I've been trying to look at is the arrangement of sperm within the spermatheca of fleas. This knowledge will have no effect on man's destiny but it intrigues me personally. I am confident no one else alive today knows how sperm are arranged in a flea spermatheca - or cares. And this idea appeals to my perverted sense of discovery."

We scientists stand on the shoulders of giants, and Dame Miriam Rothschild, who died in January 2005, at the age of 96, is one of them. There's a wonderful interview with her, David Attenborough and Prince Charles at http://www.abc.net.au/rn/science/ss/stories/s1331040.htm

The first instar monarch to crawl out of the egg is very, very tiny. Almost microscopic. Because it lives inside an exoskeleton, it grows in increments rather than smoothly. To grow, it must like a snake first shed its skin. It does this four times before becoming the final or fifth-stage larva (caterpillar.)

Myron Zalucki[27] reminds us that "first instar caterpillars are not simply small versions of later instars...it should not be assumed that because you know the biology of a fifth instar, you know the biology of the first instar." Well, no surprise there. A fifth-grader is not simply a bigger first-grader either.

The old hard head-capsule of a larva detaches itself from the rest of the cuticle (skin) just before the molting process is about to start. That's one of the first signs of an impending molt, should you want to watch the process. The new, yellowish head-capsule forms on top of it. Sometimes as the larva completes its molt you can see it shaking its head back and forth, or with anything handy rubbing itself free of the old head-capsule.

Each time they molt, the larvae shed their skin and grow. After their last molt, into the fifth instar, it's time to prepare to become a pupa, the next stage of their life. That means storing up enough food, of the right kind, and water, to become a butterfly. As the butterfly emerges from the chrysalis, it pumps its wings up with water it's stored in its abdomen, so towards the end of its larval life-stage it's eating as juicy of milkweed leaves as it can.

Hormonal changes inside the mature monarch larva also speed up. It's time for the special tissues called imaginal discs to step up to the conductor's platform and direct the orchestra. These imaginal discs began to take shape in earlier larval stages, and with proper hormonal cues now become the scaffolding for the major anatomy of the adult butterfly – one disc for each leg, one for each of the four wings, etc. First discovered in fruit-flies by Ernst Hadorn, a Swiss developmental biologist, the discs play a pivotal role in metamorphosis. Like a teenager new hormones flood the larva – growth hormone, e.g. – while others like juvenile hormone fade in their final decrescendo. These changes take several days, but if you've raised monarch larvae, you can recognize when they are near the finale and ready to pupate – they develop an obsessive wanderlust, walking in search of the right place to hang themselves.

Yes, to move onto another plane of existence, they hang themselves. Having found just the right spot – criteria as yet unknown to us — they attach themselves with a drop of homemade super-glue attached to their butt-end. They hang for a while in the shape of the letter "J." Watching the next hours in their life, as special enzymes dissolve their skin and build around them instead the chrysalis, is as unforgettable as watching a birth.

Pliny, who died in the eruption of Mt. Vesuvius on August 25, 79 A.D., describes the life history of a butterfly (*Natural History*, Book 6, chapter 37.) First the egg is formed from the sun's action on a drop of dew. "From this a small grub afterwards arises," he writes, "which, at the end of three days, becomes transformed into a caterpillar. For several successive days it still increases in size, but remains motionless, and covered with a hard husk. It moves only when touched, and is covered with a web like that of a spider. In this state it is called a chrysalis, but after the husk is broken, it flies forth in the shape of a butterfly." Except for the bit about the sun acting on dew, quite accurate, actually.

For a 21st-century record of the pupation events, see the nice set of photos at http://monarch.org.nz/monarch/2007/10/25/larva-to-pupa-to-butterfly.

In November, 2009 three monarch larvae were launched into space on the space shuttle Atlantis. (see www.monarchwatch.org/space).The purpose of the experiment was to learn the effect of development in essentially a no-gravity environment. Here's what was learned. Without gravity, larvae behaved quite normally, clinging to their food, eating, and if they did anything different, it was to spend less time eating at the top of the food provided than did the control larvae on earth. Their "J" shape, without gravity to stretch their body out, was more of a curly "C." Because of problems attaching themselves to a substrate, all three in space became "floating pupae." When emerging from the pupae (see below) the butterflies were not able to expand their wings in a normal way, though two of the three were able to fly, within the confines of the enclosed area provided them. There was some discussion online whether the results of the experiment merited sending three larvae into space, knowing that after transforming they would be unable to feed or reproduce.

We come back from space now and return to our pupa inside its chrysalis. The chrysalis of different kinds of butterflies are quite different, and can often be identified by species. In fact, for those of you who raise or find a monarch chrysalis, it can even be sexed![28] Because the pupa inside is very edible and unable to protect itself, most moth cocoons and butterfly chrysalises are painted in camouflage colors. The monarch chrysalis is a lovely pastel green. But it's design holds to me one of life's great mysteries – three tiny dots of gold spread across its top, and a line of golden droplets like an expensive necklace below. Hard materialists say natural selection is chance alone, without a guiding hand. Some find in the aesthetics of the monarch chrysalis an argument for intelligent design. No good biological explanation for their existence has as yet come forth.

For the next week or so, though from the outside the chrysalis is all an image of meditative quietude, inside it is undergoing a massive remodeling project. Though most of the larval cells themselves actually survive this rearrangement, some undergo a process called programmed cell death. This is the same process that happens to a tadpole's tail as it turns into a frog, and the tissue between our fingers at about fifty days of our own development, when our hands turn from resembling ping-pong paddles into five-fingered organs. Organelles called lysosomes release digestive enzymes which digest the larva's cells from the inside out. The molecules of life – proteins, fats, carbohydrates, nucleic acids – released by the kamikaze cells are sopped up by the surrounding tissues and the cells which have remained alive. Under the direction of the imaginal discs, which direct a complex composition in the medium of DNA expression, first the pupa forms from the larva, then from it the butterfly itself appears.

This transformation is a fascinating, complex and dangerous process. A lot can go wrong. That it is so often successful is quite remarkable.

Just as nations, schools and other institutions, and we as individuals must make decisions about how to use limited resources, so do transforming butterflies. One question that arose in some biologists' minds was: is there a competition within the chrysalis for these resources? The wings of a butterfly are its largest organ, making up some 20% of its body mass, a heavy demand on resources. In one experimental study the researchers surgically removed from late instar caterpillars the pair of imaginal discs which direct formation of the hind wings of the Buckeye butterfly *Precis coenia*. The fore-wings, thorax and legs which grew from these caterpillars were significantly larger than those which hadn't been manipulated. This suggested that there was competition within the pupa for limited resources, and if one part got less, the others got more.[29] These results also remind us that when a gene undergoes a mutation which could potentially be adaptive, if that adaptation steals resources from another part of the individual, the change might no longer be adaptive. Every monarch, whether caterpillar, chrysalis, or butterfly, is the result of millions of years of evolutionary tinkering. And like a finely-tuned sports-car engine, changing that tuning is more likely to worsen matters than improve them.

If the imaginal discs which the researchers removed are placed in a petri dish with nutrients, they fail to grow. But when the steroid hormone 20-hydroxyecdysone (the hormone which also controls molting) plus the insulin-like neurohormone bombyxin, produced by the pupa's brain, were added to the nutrients, the imaginal disk continued to grow.[30] No real surprise there: inside the chrysalis, the transforming butterfly is awash in hormones, and if it dreams at all it seems to me they must be sea-dreams.

A fair amount of work has been done on the ebb and flow of gene expression in the late-instar larva as it prepares to pupate. There's a homeotic gene called distal-less which plays a big role in the development of the particular wing pattern each species shows.[31] This gene is one of the most important in limb formation and has been well-studied in the fruit fly and other insects. Analogues of it play a part in limb formation in vertebrates like us.

One study looked at the heart of the pupa entering metamorphosis, and found that it indeed survives the process, though changed.[32] Another paper reports monitoring the heart-beat of the developing pupa, at first irregular but uninterrupted when nearing emergence into the butterfly.[33]

The next step in the life of our monarch is as fascinating as the transformation of the larva into the chrysalis. Perhaps you've been fortunate enough to have watched the chrysalis turn transparent, and see the nascent butterfly all folded up inside. That's a signal that it is about to be born – eclose, in biological terminology. And the eclosion of an adult from the chrysalis is, like all births, a marvelous thing to see, a visual choir of glorious hope and redemption.

It takes only a few hours: by scraping away at its package, the adult breaks free of the chrysalis.

The first morning of a new world.

The Roman poet Ovid recorded his countrymen's fascination with stories of metamorphosis. Birth and rebirth are themes common to much of the world's art and literature. The monarch caterpillar rests like a phoenix in its tomb, then breaks out into the light of day as a new, almost spiritual, creature. In one ode to the phoenix (*De ave phoenice*, attributed to the Roman poet Lactantius) the connection between phoenix and butterfly is made overtly.

After the fire which consumes her, the phoenix becomes a kind of legless larva:

> "...gathering into what looks like
> a rounded egg, in which she is remade
> into her former shape, bursting forth
> from her shell and springing to life as the phoenix;
> as does the larva, in the countryside,
> fastened by threads to a stone,
> to become a butterfly."

Some have seen in this transformation Christ's breaking out of the tomb. Farther back into Egyptian times the scarab beetle was given a special place of honor. The scarab larvae dig long vertical shafts into the earth where in underground chambers they transform themselves into very mummy-like pupae. These shafts and chambers are very similar to the mastaba tombs of Egypt's Valley of the Kings. Mummies were Egyptian – and Incan — pupae, supplied with food, little ships and maps to guide them to their own rebirth. Butterflies – some identified as the North American monarch's cousin *Danaus chrysippus* – are found on the walls of Egyptian tombs going back more than 5000 years.

But the chrysalis is not a tomb, it is a dressing-room in which the larva changes into its assumption-gown. The door flies open, and where was a chubby stomach on stubby legs now instead is a dream-flower, all air and angel. But as it leaves its temporary tomb, our fresh-minted monarch isn't quite ready for its first flight. Because the pupa is like a mummy, the dream-flower it holds is tightly wrapped. Before it flies it must unfold its wings. This it does by pumping water, stored in its abdomen, out through the wings' fine network of veins. And once spread, the wings must be given time to dry. Interrupting this process can derail it — the new butterfly might never fly. Again, it is walking a fine line of vulnerability.

Do enough neurons and interneural connections survive the storm of metamorphosis to allow memories of its former life to flicker like ghosts around the edges of the new butterfly's mind? We don't know, and perhaps we never can. As a biologist I'd guess only those memories would survive which are in some way evolutionarily advantageous. One study shines some light on this question. Female moths and butterflies of many species most often lay their eggs on the species of plants they ate while larvae. That's as it should be – ovipositing on just any plant might be the waste of an egg. How does the adult know what plant to lay its egg on? It could be completely hard-wired. Or does the memory of what it ate as a larva survive metamorphosis and somehow affect its choices? Larvae of the diamondback moth were fed one of three different kinds of food. After eclosing, females showed no preference for ovipositing on the particular food they'd been raised on. Nor did adult moths derived from larvae raised in the presence of neem, a chemical found in the neem tree and an ovipositing deterrent, react any differently to that chemical than from those raised without it. These results suggest that oviposition preferences are made not based on memory but are hard-wired into the adult.[34]

However some memories do seem to survive the extreme make-over of metamorphosis. Martha Weiss, at Georgetown University, provided tobacco hornworm larvae with a strong-smelling chemical (ethyl acetate), then shocked them. They soon learned an aversion to the ethyl acetate, an aversion which a large majority of individual hornworms maintained right through metamorphosis.[35]

The new-minted butterfly wakes from its sleep into the first dawn of a new world, which looks different, tastes different, smells different, and feels different than the world it once knew. It has, according to the words of Colossians 1:10-11, "taken off the old self with its practices, and…put on the new self." It has been given new eyes, a new nose, new almost everything. The world itself hasn't changed, but with their new eyes every summer all across the earth uncountable millions of new worlds are first seen, tasted, felt and smelled.

Perhaps even before it ecloses our butterfly already has had a glimpse of its new world, as though through a glass darkly. Hours before it breaks free, the chrysalis has already become transparent. Perhaps that is why it becomes transparent — to give it a glance of the world it is about to enter. If only we could get inside the brain of a monarch about to eclose, and marvel with it as that new world unfolds.

The butterfly's sensory toolbox is a different toolbox than the caterpillar's. Evolution has given each the tools most adapted to its way of life. A taste for bitter milkweed leaves becomes instead a taste for sweet nectar. Lets open up the butterflies sensory toolbox and see what's inside.

Moths mostly fly at night, butterflies in the day. One kind of butterfly that flies at night are the hyelids, which may be the "missing link" between the evolutionarily older moths and the more recent butterflies. The ability to hear ultrasounds – high frequency chirps made by bats – is common in moths. This allows them to know when a predatory bat is nearby, and take evasive action. Moths seem to have developed ultrasonic hearing at about the same time as bats developed echolocation (about 60 million years ago.) Hyelids, nocturnal butterflies, have been found to have ultrasonic ears on their wings, which they use to escape bats. These tiny ears have an eardrum set in a narrow passageway that resembles a rabbit's ear. It's been suggested that heavy predation by bats may in fact have forced some of them to fly during the day, some 50 million years ago, and in time these diurnal moths evolved into the butterflies. A certain organ of unknown function called Vogel's organ, found in various of the Papilionid butterflies, may be a vestigial remnant of their ancestor's ultrasonic ear.[36] Monarchs are diurnal. There is no evidence they can hear in the ultrasound, though there is some evidence butterflies in general have a sense of hearing, which has been very little studied.

Not only hearing, but the visual abilities of animals are closely linked to their way of life – dogs see different colors than we do, as do the birds and the bees. If you're a flying creature, distance vision is important; it's almost certain the butterfly is less myopic than the caterpillar. In general monarch vision appears to be quite poor. Chip Taylor (Dplex-l list – to sign up, go to http://www.monarchwatch.org/dplex/index.htm) reports watching a number of them as they stream down from their hibernation site fly straight into a shrine. Others have reported watching monarchs fly straight towards an object, then at about a meter's distance dodging it. We need to know more about the visual acuity of the monarch at all stages. We'll look in some detail, however, at the monarchs' visual skills which help it to migrate, in a later chapter.

In addition to its senses, evolution has issued the eclosing monarch the body it needs to survive. Wings for flying, legs for crawling (and tasting), a new digestive system to digest not leaves but nectar, the right set of senses, a long proboscis for reaching nectar, reproductive organs.

So it's no longer acceptable to just eat the table on which you walk. No, now you have to find food. Find flowers with nectar. Note to self: Look for flowers.

Well, the new toolbox helps. The world is a colorful place, and flowers make it more colorful. They're full-color ads, really. Targeting insects mostly, inviting them to stop in for a meal – and while you're there would you pick up a packet of pollen for me?

We'll see in another chapter that butterflies, like many insects, can see light's plane of polarization. Their eyes have been designed to do that. What evidence is there they can see different colors? Foraging Japanese swallowtail butterflies were trained to feed on sugar solutions placed on differently-colored disks. They very quickly learned which color the nectar was in, demonstrating both good color vision and an aptitude for learning.[37] The pipevine swallowtail shows similar abilities.[38]

Butterflies have actually shown remarkable ability to learn, given the size of their brains. Female pipevines are able to keep more than one thing in mind, something I find harder and harder to do. When trained to oviposit on a particular color of leaf, and at the same time trained to find nectar in a different color of flower, they regularly – though not always — landed on the correct color according to whether they meant to oviposit or to drink. [39]

Maureen Stanton[40] studied short-term learning in three species of butterflies belonging to the genus *Colias*. These females lay their eggs on legumes, though especially when they are new to ovipositing, they'll mistakenly land on plants that aren't legumes. During a long day of foraging for oviposition plants they get better at recognizing them and make fewer mistakes as the day goes by. But they also need to catch a drink of nectar now and then, and after searching for flowers (mostly non-legumes) to feed on before going back to egg-laying, they once again make more mistakes. Sound familiar?

The advantages of this kind of learning in insects were shown by a study which presented grasshoppers with nutritious or non-nutritious food, either placed in a predictable environment, where they could learn to go to the nutritious food source, or in a random environment where learning was impossible. Individuals grew faster in the predictable environment, which allowed them to learn and select nutritious food.[41]

Though we can't, many insects can see in the ultraviolet. If you put on ultraviolet-sensitive glasses, the world of flowers leaps into a whole new dimension of beauty. There are lines and circles on flower petals written in ultraviolet ink invisible to us but which direct pollinators inward towards the nectar and pollen. One species of lupine, *Lupinus pilosus*, is pollinated by bumblebees. After a bee visits a particular flower, the flower changes color, indicating to other foraging bees that the nectaries, like an ATM out of cash, have been emptied. Manually manipulating the pollen-release mechanism of the flower causes the same color-change, and bees preferred flowers which had not yet changed colors.[42]

Flowers are butterfly restaurants. What criteria does a butterfly restaurant critic use for rating these restaurants? It must have nectar, preferably 20-25% sugar, within reach of the uncoiled proboscis. But the nectar should have a dash of amino acids, too, and some nutritious minerals. And a comfortable landing pad to rest on while eating would be nice.

Though nectar is a favorite food, butterflies will eat other things to meet their nutritional requirements. They've been seen drinking tree sap, sopping liquid from wet soil, gourmandizing on pollen, rotting fruit, mushrooms, carrion, dung, bird droppings, urine, sweat, and slug slime. And that's only page one of the menu. There are others, some positively unappetizing (to us.) They can't chew their food but if they can drink it or lap it up in some way, and it's got what they need, they're not shy at the table.[43]

Males meanwhile also look for the chemicals — or their precursors — they'll need to either attract a female, or build their nuptial gift (more on that, later.) So it's most often males found in "puddle clubs," clustered at puddles of urine, feces, or carrion. Males of a cousin of the monarch, the queen butterfly, land on the dry head of a floss-flower, moisten it with saliva, then sop up the mix of chemicals they need to synthesize their sex pheromones. That's because if they don't got enough sex pheromones, they don't get enough….well, you get the idea.

When we first learn about animals most of us are told there are two kinds: warm-blooded and cold-blooded. The blood from one feels warm, from the other cold. It's true, on a chilly May morning the blood of a rabbit is warmer than the blood of a snake. But later that afternoon, if the snake's been basking in the sun, its blood might be warmer than the rabbit's.

So let's improve our definition of warm-blooded. Warm-blooded creatures have body temperatures which don't vary, while cold-blooded body temperatures track the ambient (environmental) temperature. Better, but still not right. We're warm-blooded, you and I, and our own body temperatures do vary, often by several degrees Fahrenheit over the course of a day. Most of us are coolest in the morning, after our metabolism's been dialed down while we slept, and warmest in the afternoon, after we've been busy all day. And of course if we have a fever our body temperature can go up pretty drastically.

Meanwhile many "cold-blooded" creatures can have body temperatures that are quite different from ambient. If it's really hot in the desert, say one hundred forty on the sand, insects, snakes and lizards find a shady place to cool themselves, or burrow into cooler earth. Or if it's a cool desert morning, forty degrees Fahrenheit, they might bask in the early morning sun, picking up energy from its rays and warming themselves. They have a repertoire of strategies for warming, which includes physical activity that generates metabolic heat. Many of these "cold-blooded" creatures have anatomical or physiological means of using or losing metabolic heat. Moths studied by Bernd Heinrich can shunt blood flow to dump metabolic heat if they need to, or keep it near their wing-muscles, if they need it.

So, like most things in biology and life in general, there are exceptions to prove the rule. The rule, then, restated, becomes this: Warm-blooded creatures (endotherms, also called homeotherms) have body temperatures which vary less, usually considerably less, than cold-blooded creatures (also called ectotherms, or poikilotherms.)

Insects like bees and butterflies can't fly when their body temperatures are too cold — their muscles and neurons just don't work well. So as the thermometer follows the setting sun bumblebees sometimes get stuck on, and overnight on, the last flower of the day. But there's plenty of evidence that insects shiver, flutter their wings, or bask in the sun to warm up on chilly mornings.

If they could set the outdoor thermostat, what range of temperatures would a monarch prefer? Well, as larvae, they'd want it somewhere between 10C and 35C (about 45 – 95 F). Outside those temperatures they can't survive for long. Adults can survive a much greater range, from as low as -14C to 41C (7 to 106 F.) But they're only able to fly between about 12 and 40C (54 and 104 F), and they really don't like temperatures above about 33C (90F.) In spring, once the temperature in the more southern states they're passing through rises consistently above that, they head north. On really hot days they run the risk of overheating, and will spend considerable time resting in the shade. If they absolutely must fly in those temperatures, they prefer to glide rather than flap.

Females lay their eggs on the bottom side of milkweed leaves to be less visible to predators, but they choose plants that are exposed to the sun's warmth for a good part of the day, so the eggs develop more rapidly. Larvae appear to bask, and can gain eight degrees C or more doing so, reducing their development time by as much as half. If they become overheated they've been seen to crawl down the plant onto the cool earth, or into the shade. The larvae have also been seen to behave as though they are sleeping. They'll sometimes hang their heads and go into a quiescent period. Barbara Case (Dplex-l list) has posted a photograph of several of the caterpillars in a shoebox nicely lined up, as evening comes on, dozing off like tired monks in a monastery at: http://www.flickr.com/photos/8812810@N02/773429215

When they're flying, monarchs generate significant quantities of metabolic heat, just as we do when we're exercising. A butterfly's excess heat is efficiently carried away by air currents as it flies through them, so unless its very warm (above 90 F), they don't overheat. On the other hand there are times when they do need to heat themselves up to operating temperature. Like their larvae, many butterflies bask in the warm sun to heat themselves. I recently watched a mourning cloak do just that, on a mid-March sunny day in northern Wisconsin. It had found a slope of lawn that set it at just the right angle to optimize its solar gain.

Adult monarchs also bask. While doing so it appears that their wings do not act as solar panels; basking is warming their body, not their wings, though the wings do help produce still air around them to prevent convective heat loss. The wings are also used as reflective panels to reflect solar energy to the body, where there is a coat of heavy hair-like scales on the thorax to act as insulation and retain the heat. At the same temperature, males seem to have higher metabolic rates than females, and reproductive individuals higher than diapausing (migrating) individuals (Dr. Chip Taylor, Dplex-l list.)

Moths, mostly nocturnal creatures, find little gain from basking in moonlight, and have instead evolved the ability to shiver to warm up. Monarchs are one of the few butterfly species known to shiver. Shivering warms the body about the same rate and uses about the same amount of energy as flying.[44] At around 15 C (60 F), by shivering they can warm their thoraxes by about two degrees Fahrenheit a minute.[45] Once their thoracic muscles are properly warmed they can launch into the air, confident that flying itself will keep them warm.

Because development is so temperature-dependent it's possible to make some interesting predictions about how long development will take and how many generations can develop at different latitudes. A degree day is one day one degree above the lowest development threshold for an insect, which for monarchs is 11.5 degrees C (53 degrees Fahrenheit.) Since the egg requires about 45 degree days to hatch, at 12.5 C it would require 45 days – a long time! You can do the calculations for hatching time at different temperatures, and if you're a teacher, it's a good way to link math to biology. Though there seem to be more than one opinion on the exact answer, it takes about 200 degree days from egg to pupation, and 700 degree days for a newly-laid monarch egg to hatch, develop as a larva, pupate, eclose, and for that female to lay her first egg. Seven hundred degree days, egg to egg. In Winnipeg, which for the years 2003-2006 averaged around 1500 degrees days up to the end of September, that's a total of two generations. In St. Paul it's perhaps three, in Dallas more like six. An unusually cold summer can change all that, and global warming, should it continue, is likely to also.[46]

If our new adult monarch – first morning of a new world – is in the first generation of that summer's to eclose in the northern part of the U.S., it will become a reproductive adult. Its children are likely to, also. But as the long days of high summer wane towards August and September, it would do no good to try to reproduce. Eggs laid that late would not become adults before the hard killing frosts of October. Instead of reproducing, generations which eclose in the later parts of summer migrate. And migrating monarchs live much longer than reproducing individuals – reproductives, two to six weeks, migrators six to nine months.

How they "decide" which to do is an interesting story.

It's a story about hormones, mostly.

Juvenile hormone (JH), for one. In us, what we call the "sex" hormones – estrogen and testosterone, e.g. – play a big part in puberty and achieving reproductive maturity. In insects it's juvenile hormone that plays that role; without it, the gonads and auxiliary organs simply don't mature. Female monarch ovaries grow rapidly after eclosion, for about a week, as do the male sex organs. This is correlated with an increase in JH, which peaks in females three days after eclosing, then gradually declines.[47] In females the brain plays a part in sexual maturation, by producing hormones which stimulate the production of an important yolk-protein, vitellogenin.[48]

But maintaining high amounts of JH, ironically, accelerates old age, presumably by increasing metabolic rate. The increased lifespan of migratory monarchs appears to be due to down-regulation of juvenile hormone. Injecting JH into migratory individuals decreases their lifespan, and preventing JH synthesis by removing the corpora allata of non-migratory individuals increases their lifespan by up to100 %.[49]

Monarchs who eclose in the shorter days of early August, when the milkweed quality has begun to decline and the nights are cooler than they had been, produce less JH. Less JH prevents them from becoming reproductively mature, and kicks them instead into migratory behavior and the longer lifespan that comes with that.

In Minnesota many individuals become the migratory type by the third week of August. By early September all or nearly all of both sexes are in reproductive diapause.[50] Monarchs fed old milkweed reached diapause before individuals fed young plants. There's a kind of hurry-up, we need to leave quality to this switch. Even development from egg to adult speeds up near the end of summer, probably because of lower titers of JH.[51]

Two additional hormones that move a monarch to be migratory are neuropeptide hormones, small proteins produced in the brain. One, adipokinetic hormone, elevates fats in the hemolymph, useful for fueling migration. The other is monarch diuretic hormone, which accelerates water loss after eclosion. To the migratory individual, any excess water left after the wings have been expanded is just extra weight to carry on the long trip ahead, weight which is not as critical if you're reproductive.

The switch from being a reproductive individual to instead becoming migratory, controlled by hormones, seems to depend on a number of environmental clues. The decreasing day-length of late summer seems most important, with the fluctuating temperatures which occur at high latitudes at that time and decreasing food quality also playing a part in urging diapause.[40]

In Christian theology, death is more than an unending bodily diapause. It is a kind of transformation, a kind of undressing, as we take off the lineaments of mortality to put on instead our "assumption gowns." But death also reminds us that not all transformations are for the better. Peace sometimes becomes war; compassion, hatred. Death came every day, more common than the dawn, to Nazi concentration camps. The human mind and spirit can wither before the body. The world held little beauty to the inmates of the camp called Terezin, who experienced instead disease, death, and a weary day-by-day grinding down of body, mind and spirit. Some 15,000 children suffered and died there, or after being shipped to a death-camp. Only a hundred survived, none younger than fourteen. While at Terezin some communicated their feelings in paintings or sketches on walls or scraps of paper. Friedl Dicker-Brandeis, a small, fragile woman, dedicated her life to teaching the children of Terezin to find what little joy they could through art. Others wrote their feelings in short but touching poems. Pavel Friedman[52] was twenty-one when on June 4, 1942 he wrote this poem. He would live a little over two more years yet before dying at Auschwitz.

The Butterfly

The last, the very last,
So richly, brightly, dazzlingly yellow
Perhaps if the sun's tears would sing
against a white stone…
Such, such a yellow
Is carried lightly way up high.
It went away I'm sure because it wished
to kiss the world good-bye.

For seven weeks I've lived in here,
Penned up inside this ghetto.
But I have found what I love here.
The dandelions call to me
And the white chestnut branches in the court.
Only I never saw another butterfly.

That butterfly was the last one.
Butterflies don't live in here,
in the ghetto.

In late 2009, the Holocaust Museum announced it was collecting 1.5 million handmade butterflies to represent the same number of children who died in the Holocaust.

Butterflies are dream-flowers, emblematic of beauty and freedom and unending possibilities. The choices made for monarchs – to undergo metamorphosis, to become reproductive or to migrate to a distant land — and the choices they themselves make – which plant to oviposit on, who to mate with, where to spend the night or which flower to sip from – remind us of the opportunities life gives us to transform and fly. As a species, it's time we thought about who we are and who we've been and who we want to be. Perhaps its time to choose which we'd rather be, the single-minded eating machine or the orange and black dream-flower, transform ourselves accordingly, and in so doing free other species from the death-camps we sometimes transport them to.

Monarch of the Butterflies describes in detail the life story of this, one of the best-known and most-loved of nature's creatures. In it the author introduces us to what we've learned from and about the monarch, through science, literature and art.

Monarch of the Butterflies