The Butterfly Clock:
Illuminating the Molecular Mysteries of Monarch Migration

by

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A.B. Biological Sciences
Smith College, 2006

SUBMITTED TO THE PROGRAM IN WRITING AND HUMANISTIC STUDIES IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE IN SCIENCE WRITING
AT THE
MASSACHUSETTS INSTITUTE OF TECHNOLOGY

SEPTEMBER 2007

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Submitted to the Program in Writing and Humanistic Studies
on May 7, 2007 in partial fulfillment of the requirements
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ABSTRACT

Each fall, the entire monarch butterfly population of the Eastern United States and Canada funnels into a handful of oyamel pine groves in Michoacán, Mexico, to weather the winter months. Each spring, the butterflies mate and fly north to repopulate the continent in short generational bursts. The monarchs flying south in the fall are three generations removed from those that made the trip the previous year. With no parents to guide its way, a migrating monarch has only its genes to steer it to its Mexican overwintering site.

Monarchs orient using the sun as a guidepost. Because the sun appears to move across the sky throughout the day, the butterflies must keep track of time in order to correctly interpret the sun's position. Although this so-called "time-compensated sun compass" was demonstrated in 1997, little was known about how it worked. Steven Reppert, a neurobiologist at the University of Massachusetts Medical School in Worcester, MA, is working to change that. His lab seeks to understand the cellular and molecular mechanisms monarchs use to guide them on their remarkable yearly journey.

Reppert and his colleagues believe they have pinpointed the sun compass, and the circadian clock that guides it, in the monarch brain. They have shown how the clock and compass might work together to allow the monarchs to find their way to Mexico. Their work has also uncovered some unexpected insights into the workings and evolution of circadian clocks in general. This thesis profiles these discoveries, exploring how circadian biology has illuminated monarch migration, and how monarchs, in turn, have illuminated circadian biology.

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High in the mountains of central Mexico, in the cool mid-morning shade, a remote oyamel pine grove seems ravaged by some exotic blight. On every tree, huge branches appear to droop with dead foliage, sagging drably toward the forest floor. But once the sun sneaks its rays past the pine needle curtain and bakes the winter bite out of the air, the pendulous branches suddenly bloom. Gray unfolds to reveal splashy orange, as if millions of dead flowers are coming inexplicably back to life.

Only the foliage isn't foliage, dead or blooming. The petals of this improbable January bloom are the wings of monarch butterflies—hundreds of millions of them, unfolding from their cozy winter clusters to welcome the sun's warmth.

As the sun climbs upward, the huddling butterflies ruffle and sway. Individual butterflies peel off to join a burgeoning swarm. They crackle above their bright clusters like sparks above a flame. Beyond the trees, the sky is ablaze with monarchs.

These butterflies, the legendary winter residents of the El Rosario Monarch Butterfly Sanctuary in Michoacán, Mexico, draw a sizeable crowd of human spectators. Groups of weekend tourists straggle up the trail to the groves, perhaps two miles from where they left their cars or buses. It's slow going in the meager mountain air. The path, mostly paved, is a rambling slalom of steep slope and stairs.

On one warm Saturday, Tom Emmel, undeterred by the altitude and the grade, is determined to reach the butterfly clusters before the sun does. This is the twenty-seventh consecutive year that the University of Florida entomologist has visited the monarch groves in Michoacán. As he increasingly does on his frequent expeditions around the globe, Emmel has a flock of enthusiastic followers in tow—myself included. After outfitting a few group members with walkie-talkies Emmel charges ahead. We slower folk, with our aching legs and griping lungs, won't see him again until the top of the trail.

As we hike, we chatter excitedly. Most of the group have never been here before. We've seen summer monarchs emerge from their chrysalides on our backyard milkweed, perhaps. Or we've seen fall monarchs bed-and-breakfast in our butterfly bushes on their way through town. We have no idea what's in store for us.

After five hours on a plane, five hours in an airport, five hours on a bus, and a freezing night under damp wool blankets in the mountain town of Angangueo, I'm ready to see some butterflies. Soon enough a monarch floats across my field of vision like one of the blobs of light that dance across closed eyelids—try to focus on it, and it's gone—then there's another, and another. I'm wondering, is this it? Is this the spectacle? Then we turn a corner at the top of a steep grade, the forest spits us into a meadow, and in an instant the entire journey is consummated.

It's an orange-out the way a blizzard is a white-out. A river of monarchs gushes from the trees beyond the shrubby meadow, then tumbles and swells through the clearing. It sounds like a river, too—a layered roar composed of a million whispers. As the butterflies careen past me, ricocheting off my face and shoulders, they make the crinkling noise of a candy wrapper surreptitiously torn open. They pause en masse, quivering on the ground, to drink from a rivulet that bisects the meadow. They perch on bushes and people, dusting everything with a coating of orange.

We each inadvertently draw in our breath as we enter the scene. We experiment with adjectives, but can't find any that felt apt. Awe-inspiring. Spectacular. Majestic. They fall impotently off our tongues so we quiet ourselves and simply look.

Emmel's voice over the walkie-talkie tells us to keep trekking. We plunge back into the forest at the opposite end of the meadow and hike a few minutes more. Emmel is waiting where the trail ends, peering past the rope cordons that keep us from venturing further into the trees. I follow his line of sight to the butterfly clusters themselves. This is the source of the orange river that flooded the meadow below. Monarchs hang by the millions, in odd fungus-like clumps that bloom improbably into the sky.

"I know there's all this wonderful science behind it," a woman says to her companion after several minutes of silence. "But it's still a miracle."

What does she mean by the word? What makes this experience so ineffably superlative? As I stare up through the butterfly blizzard into the blue beyond, I think about what it took for the monarchs to get here. Some of them traveled thousands of miles from their birthplaces. Whereas our arduous journey took a couple of days, theirs took a couple of months. And all of them bear the imprint of millions of years of natural selection. Evolution shaped and painted the form our eyes find so pleasing, and patterned the yearly migration that fills such a tiny haven with such staggering numbers.

Maybe miracle is the word, in that it captures the goosebump-worthy awe we feel as observers. But it's not a miracle in the divine sense. It's not a miracle *despite* the science. As scientists work to understand what compels monarchs to migrate, they are unearthing molecular secrets as moving and mesmerizing as the orange blizzard before us. If there's a miracle, it's to be found *within* the science.

Spectacular biology

"For the most part people have just looked at monarch migration and called it a mystical event," says Steven Reppert, a neurobiologist with a soft spot for insects. Reppert staunchly rejects the idea that there's anything magical about the butterflies' yearly trek. "There's a biological basis for it," he says. Coming from Reppert, this statement is anything but dismissive. "It's spectacular biology," he adds.

Reppert's office at the University of Massachusetts Medical School in Worcester, Massachusetts, is probably best described as L-shaped. But with a little imagination the legs of the L could be the outspread wings of a butterfly. We're sitting at a round table—a spot on the right wing. And we're leaning over his sleek little MacBook—itself a pair of unfolded wings. It's easy, in Reppert's presence, to see butterflies everywhere.

Reppert gestures towards a map on the screen of his laptop. It's the familiar shape of North America, shaded red wherever eastern monarchs spend their springs and summers. The United States is more red than not. The western border of the red zone roughly traces the continental divide, following the Rocky Mountains northward from New Mexico up through Montana; the eastern border is the Atlantic Ocean. Red surges into Canada, from Quebec to Alberta, with the tiniest, northernmost finger jutting up into British Columbia.

But what's most remarkable on Reppert's map, pinched from a monarch-themed website, is not the dizzying expanse of red. It's a miniscule spot of yellow, which I have to squint to see. This spot marks the monarchs' overwintering grounds, the endpoint of their yearly migration—those remote oyamel pine groves in the mountains of central Mexico where I stood slack-jawed and stared into a blizzard of butterflies. Each year, the entire eastern monarch population crowds into those groves to weather the cold season. As fall cools into winter, hundreds of millions of butterflies funnel southward from the red zone into the yellow: from well more than three million square miles into just three hundred. There, they huddle in tight clusters until spring arrives. The microclimate in these montane forests is like Goldilocks' porridge: just right. It's cool but not too cold; damp but not drenched; the conditions are perfect to keep monarchs alive through the winter.

In early March, when winter begins to wane, the sun coaxes the overwintering monarchs out of the trees. By then these winter butterflies, in monarch terms, are Methuselahs; at seven months or so, they are far older than any summer monarch will ever be. They live so long in part because nature pressed the pause button on their sexual development. Winter held them in limbo, in a state known as reproductive diapause. But as spring approaches, for the first time in their lives, they are stirred by the urge to mate—and they do so, in a massive flurry of color, countless orange wings against crisp blue sky.

Meanwhile, each butterfly's internal compass has rotated, its needle drawn in a new direction. Whereas in the fall they were compelled to fly south, now they are drawn irresistibly to the north. It's time to find milkweed, the only plant on which monarchs will lay eggs. As soon as they emerge from their chrysalides, the newborn summer monarchs are ready to mate, unlike the southward migrators. Their life cycle is short and efficient: they hatch, metamorphose, take wing, mate, lay eggs, and die—all within the span of about two months. This northward leg of the annual migration is a relay race, each short generation handing the torch to the next. In this fashion, the butterflies burst forth from their overwintering sites and fan out into their summer range, repopulating that wide red swath on Reppert's map.

The first northbound summer generation, hatched from eggs laid by the butterflies that flew south and wintered in Mexico, begets a second. The second may even beget a third. So when fall arrives, a monarch emerging from its chrysalis at the northern edge of its range is the grandchild or great-grandchild of those that flew south the previous fall. Its impending trek to Mexico will be its maiden voyage. "You're talking about butterflies that are three generations removed—the ones that make the journey from the ones that were there before," Reppert explains.

If someone dropped you off in Canada, could you find your way to Michoacán, Mexico? What if you had never been there before, or even heard of the place? What if you had no map, and no one to guide you? What if your brain was no bigger than the head of a pin?

This is exactly what monarch butterflies do each fall. They journey toward Mexico for the first time in their lives, with no parents to show them the way. And that, Reppert says, is what's so mind-boggling about monarch migration. "They really are traveling there for the first time, and there's nobody who's telling them how to get there," he says, a slow smile spreading across his face. Because of that, he says, "there has to be a genetic program that is underlying the vast majority of what these animals are doing." If they can't learn the route from their parents, they must learn it from their genes. That fantastic funneling, from the vast red smear across North America to the tiny yellow dot in Mexico, must somehow be imprinted in their DNA. And Reppert wants to figure out how.

How does a butterfly with a 4-inch wingspan navigate thousands of miles to a precise destination? The insects need a guidepost to keep them on track, Reppert says, and the most reliable guidepost for daytime flight is the sun. So they set their course according to a so-called sun compass.

But it's not as simple as following the sun. As the earth rotates about its axis, the sun appears to move across the sky from horizon to horizon, east at dawn to west at dusk. The butterflies' guidepost is a moving target, but their destination is a fixed point.

For most of their journey to Mexico, the butterflies need to steer a steady course to the south-southwest. In order to do so using the sun, they need to know what time of day it is. In the morning, they must steer to the right of the sun, at noon they can head almost straight for it, and in the afternoon the must steer to the left. To steady its needle toward Michoacán, the monarch's internal compass must constantly re-calibrate itself to compensate for the sun's movement over the day. "And the way that they've learned to do that," Reppert says, "is to use their internal clock."

Monarchs, like almost all living beings, have an internal timepiece, called a circadian clock, that keeps track of the time of day. The clock and the compass cooperate in the monarchs' pin-sized brains to form a remarkably sophisticated navigational device that biologists call a "time-compensated sun compass"—a compass that adjusts itself over the hours.

Biologists long suspected that migrating monarchs used a time-compensated sun compass, as honeybees and desert ants were known to do. Many had attempted to prove it. But as recently as a decade ago, no one could say for sure. So in 1996, University of Arizona biologist Sandra Perez, working with Orley Taylor and Rudolf Jander at the University of Kansas, set out to verify that the monarch's compass was guided by its clock.

To demonstrate that time of day dictates how monarchs orient themselves, Perez and her group started by confusing the butterflies' clocks. They kept one group of monarchs on a normal schedule of sun-up and sundown. Another group they "clock-shifted" by manipulating their light schedule—effectively giving them jet lag. For these monarchs, both dawn and dusk came six hours later than for the normal group. It was as if the normal monarchs were on Central time, and the clock-shifted monarchs closer to Hawaii time—when in reality all the butterflies were in a lab in Eastern Kansas.

Perez predicted that when she released the clock-shifted butterflies outside, they would be confused about what time it was and would misinterpret the sun's position. It might be 3 PM outside, but it would be 9 AM as far as the altered monarchs were concerned. So instead of steering to the left of the afternoon sun, they should aim to the right of what to them seemed like the morning sun. Their bearing should be spun clockwise from that of the normal butterflies.

One by one, Perez, Taylor, and a gaggle of graduate students released the lab-bound monarchs into the autumn Kansas sky. With compasses in hand, they chased after them, estimating and recording the direction they flew. Five hundred thirty-two monarchs later, Perez crunched the data, plotting each butterfly on the face of a compass. And sure enough, on average, the baffled monarchs spun clockwise from the normal ones, pointing just north of west instead of just west of south—bound incorrectly for California instead of Mexico. The normal butterflies could follow their internal sun compass south-southwest to their overwintering grounds, but only because the clocks in their brains kept proper time. For the clock-shifted monarchs, a faulty timepiece meant a faulty compass. Perez and her group published their findings in 1997 as a page-long correspondence in *Nature*, one of the premier scientific journals.

Perez remembers that fall—those days spent chasing butterflies—with fondness. "There was just this hysteria of monarchs in the air," she recalls. "It was an all-consuming passion at that time." She recounts their approach with a touching dose of self-deprecation, interrupting her own stories with contagious laughter. "We submitted it to *Nature* because we were full of ourselves," she explains. But in the end, Perez downplays her own role in the discovery. "It was such an obvious question," she says, but as a newcomer to the field she didn't have a sense of how intractable it had been to other researchers. "I didn't know that it couldn't be done," she explains, "so I did it."

Simulating flight

Whereas Perez chased butterflies through a sunny field, Reppert and his group watch them on remote surveillance cameras from an air-conditioned hut as the insects flap their ineffectual wings in a butterfly flight simulator.

Reppert had the University of Massachusetts Medical School build him this hut, situated in a vacant field a couple miles from the building that houses his office and lab. The field belongs to the Worcester Foundation—once an independent biomedical research institute, famous for developing the first birth control pill, but now an offshoot campus of the Medical School that mostly hosts retreats and conferences.

On a chilly fall afternoon, Reppert's lab manager Amy Casselman drives me out to the facility in her aging Subaru. The air has a wintry kick and the sun is flirting with the western horizon. December will be here soon. The monarchs that hatched in Massachusetts in September, or passed through in October, are just now arriving at the overwintering sites in Mexico.

Casselman parks in front of a hideously ramshackle building that she calls, with equal parts affection and disgust, the Sheep Barn. The building is as dingy as the main campus lab is modern. I eye the peeling paint and barred windows as we step through dusty air into an unlit atrium with rough plywood floors. We clamber through the darkness, past hulking piles of unidentifiable junk and into a tiny room.

The room turns out to be a miniature lab, an incongruously tidy chamber in the otherwise filthy innards of the Sheep Barn. It is dominated by three giant incubators where monarchs are housed in preparation for experiments. Casselman and her colleagues found that the monarchs would injure themselves and each other if they were given room to flutter around inside the incubators, so now they file the butterflies in glassine envelopes like index cards—still alive, but with their wings folded and restrained. The butterflies take their meals from within the envelopes, their proboscises poking out while their wings stay folded. Inside the incubators, the lights flick on and off at regular intervals: automated dawn and dusk, as programmed by the experimenter.

Along one wall runs a lab bench where the monarchs, fresh from the incubators, are prepared for the butterfly flight simulator. It's too late in the season for these test flights, but Casselman opens one drawer after another to show me the tools of the trade. Often it's Reppert himself who wields these tools, outfitting the butterflies for simulated flight; unlike many senior researchers, Reppert is known to join his lab members in the trenches, getting his hands dirty with the actual grunt work of research. Once a butterfly has been acclimated to the light-dark cycle in the incubator, Reppert removes it from its glassine envelope. Cradling the insect in one hand, he pierces its thorax with a syringe needle. He then carefully threads the hooked end of an inch-long tungsten wire into the hole, and secures it in place with a tiny dollop of beeswax. Thus equipped, the butterflies are carted out to the field behind the barn where the experiments are conducted. There, they flutter about in big mesh cages, acclimating to the sunlight and to their odd new appendages, before taking their turns in the butterfly flight simulator.

The much-hyped simulator is humbler than I expected. Cobbled together from clunky plastic parts, it looks like it would fit right in at a high school science fair. To place a wired monarch into the simulator, Reppert plugs the other end of the tungsten filament protruding from its thorax into a device that can measure and record what direction the butterfly is facing. The recording device is suspended over an opaque plastic barrel.

From beneath the anchored insect, a fan blows straight up through a bundle of plastic drinking straws. The fan is meant to simulate a thermal—a column of rising air on which a migrating monarch might hitch a ride—and the drinking straws serve to even out the flow and direction of the air current.

Stirred into flight by the simulated wind, the tethered monarch tucks its legs up close to its body and flaps its wings. Dangling into the belly of the barrel, it can only see a small wedge of sky. While it can flap its wings and rotate freely, it can't move forward or backward, up or down. It can twirl itself toward Mexico, if its clock and compass tell it to, but it can't move an inch.

As the monarch steers, the tungsten wire protruding from its thorax rotates along with it, telling the recording device which way the butterfly is "flying." The recording device sends this directional data to a computer, which creates a virtual flight path for the butterfly. A monarch will flutter inside the plastic barrel for hours on end, seemingly unperturbed by the tether.

At the base of the barrel, the pinhole-sized eye of a surveillance camera peeks up at the butterfly. The camera lets the researchers see the monarchs without the monarchs seeing them. This allows them to verify when the monarchs are actually flying. During an experiment, the flight simulator perches on a platform in the open field, while the researchers hide on the sidelines in their custom-built hut. Camped out in the hut, Reppert can monitor the monarch's flight the way a bank security guard monitors a video feed of the vault. Tethered into place in the middle of a wide-open field, the monarch can see only barrel and sky. It has only the sun, streaming into its butterfly brain through the facets of its compound eyes, to guide its compass.

The idea for the flight simulator—and the blueprint—came from Queen's University in Ontario. Unlike Sandra Perez, neuroscientist Barrie Frost didn't put much stock in chasing butterflies. When Perez's 1997 *Nature* paper came out, Frost was skeptical of her methods. Together with Henrik Mouritsen, then a postdoctoral fellow in his lab, Frost set out to construct a device that would allow them to probe, under more tightly controlled conditions, the strategies migrating monarchs use to orient themselves. First in the hands of its Canadian inventors, and later in the overgrown field behind the Massachusetts Sheep Barn, the butterfly flight simulator would drastically change the kinds of questions researchers could ask and answer about monarch migration.

The first question Frost and Mouritsen tackled with their new instrument was the time-compensated sun compass Perez claimed to have revealed. In the fall of 2001 they collected about sixty monarchs from the northern shore of Lake Ontario, all in reproductive diapause and ready to begin their trek to Michoacán. Like Perez, Frost and Mouritsen kept some monarchs on a schedule mimicking the local timing of sun-up and sundown. And like Perez, they tinkered with the internal clocks of the other monarchs. One group they advanced, so that dawn and dusk came six hours sooner. Another group they delayed by six hours. But unlike Perez, who estimated flight direction by eye, the Canadian group was able to measure the flight path of each tethered monarch precisely over an hour or more. And unlike Perez, they were able to rule out possibly interfering influences, such as wind and geographical features.

Frost and Mouritsen came to the same conclusion that Perez did: migrating monarchs navigate using a time-compensated sun compass. They published their results in *Proceedings of the National Academy of Sciences* in 2002. Given the added controls their simulator afforded them, they claimed right of discovery for the monarch's time-compensated sun compass. Perez's 1997 study was probably incomplete, but whether it was altogether invalid is a matter of debate. "A lot of people threw stones at this study," Reppert recalls. But whatever the failings of her approach, Perez was onto something. "She got it right," Reppert says. His voice is laced with excitement over the result—even now, a decade later—as well as exasperation with the naysayers. Reppert believes that Frost and Mouritsen confirmed, rather than supplanted, Perez's study. "Give credit where credit is due," he says. "And she deserves it."

In 2003 Reppert and his colleagues, using the Frost-Mouritsen flight simulator, confirmed the result yet again. They also took their study one step further. To be sure the time compensation could be traced to the circadian clock, Reppert decided to throw a wrench into the butterflies' clockwork and watch what happened. Oren Froy, then a postdoctoral researcher in Reppert's lab, found that it was possible to break the butterflies' clocks by keeping them in constant light, as if the sun never set. Under those circumstances, Reppert says, "the molecular gears of the clock are frozen." After a few days in constant light, the butterflies could no longer tell time.

When their clocks ticked properly, the butterflies interpreted the sun's position based on what time of day they perceived it to be. But when their clocks ground to a halt, the butterflies flew straight for the sun. Their compass needle was still drawn toward the sun, but without a clock the monarchs couldn't adjust for time. "It's as if without the time-compensated component, the butterflies would just follow the sun from east to west," Reppert says, "and they'd never get where they want to go."

So not only did shifting the butterflies' clocks shift their compass bearing, but stopping their clocks altogether rendered the compass useless. The verdict was in: migrating monarch butterflies use a time-compensated sun compass, modulated by the circadian clock, to steer them toward their Mexican overwintering sites.

The sun compass

Any given butterfly in the orange sea at the El Rosario sanctuary followed the sun to get there, adjusting its bearing throughout the day as its circadian clock marked the passing hours. Across hundreds or thousands of miles, it took wing each morning and steered in the southwesterly direction its compass dictated. But if the butterflies are using a sun compass, how exactly can the compass tell where the sun is?

Insects can perceive sunlight, as it enters their multifaceted eyes, in a few different ways. First, and most obviously, they can respond to the intense and singular shining disc of sun itself. But they can pick up subtler light cues as well.

When a ray of light radiates from a source, its electromagnetic waves vibrate perpendicular to the direction it travels. Light from the sun is not polarized, which means that its rays vibrate in all possible directions: up and down, side to side, and everything in between. When sunlight nears the Earth, however, atmospheric particles get in its way. These particles polarize the light, constraining it such that it can't vibrate in as many directions.

Skylight is polarized to different degrees depending on its location in relation to the sun. This means that the sky has distinctive polarization patterns, much like the distinctive ridges of a fingerprint. Our relatively insensitive eyes can't perceive these patterns. But some insects have specialized structures in their eyes that can detect the strength and direction of polarized light. What's more, these skylight polarization patterns change over the course of the day.

Skylight is most polarized at a 90-degree angle from the sun. So at noon, when the sun is high in the sky, the most polarization occurs at the horizons. At sunrise and sunset, when the sun is near the horizon, the most polarization occurs at the zenith (the point in the sky directly above an observer's head). If the sky polarization pattern is like a giant fingerprint, it's the print of a finger that's following the sun across the dome of the sky from one horizon to the other. By sensing the pattern of polarized skylight, an insect can pinpoint the sun's position throughout the day, even if the sun itself is obscured.

Bees, for instance, use the pattern of polarized skylight to help them navigate, or when communicating directions to other bees. Ants, too, use a polarization compass to find their way back to the nest after foraging for food. But how do these compasses work?

An insect's compound eye is a collection of many "simple eyes"—thousands, in the case of butterflies. Each simple eye contains several light-sensing cells with many finger-like structures called microvilli, which contain the pigments that allow the cell to sense light. Individual light-sensing cells are highly organized. All the microvilli are lined up in parallel, all pointing in the same direction. Even within each microvillus, all the pigments are lined up in parallel. This precise geometry means that light vibrating parallel to the microvilli is absorbed most strongly. As a result, the cell can detect whether light is polarized.

But throw several cells together in a simple eye and they create a disorganized structure, with microvilli pointing in random directions. Even though each individual cell is sensitive to polarized light, the haphazard collection as a whole is only marginally sensitive. The randomness, for the most part, cancels out the effect. From the insect's point of view, this is a good thing. While some degree of polarized light vision might help it sense its surroundings, too much would interfere with normal color vision. The random microvillus organization also makes for a more complete visual sampling of their surroundings.

In many insects, however, there is a region of the compound eye—called the dorsal rim area, or DRA—where randomness does not prevail. The simple eyes in this region, at the topmost edge of the compound eye, have an unusually regular geometry.

Imagine several people forming a rectangle, facing inward. Each person represents a light-sensing cell, and her fingers represent the pigment-containing microvilli. Each person extends her arm straight in front of her, with her palm facing down, so that her fingers are parallel to those of the people opposite her. All fingers now point in one of two directions—and those directions are perpendicular to each other. In this configuration, not only is each hand highly organized, but the collection of hands is highly organized too. This is the structure of the simple eyes in the DRA. The precise geometrical arrangement, with microvilli at right angles, means that these simple eyes can keep track of polarization. They can tell whether incoming light is polarized, and if it is, they can tell which direction it's vibrating.

Specialized DRA structures are critical for insects, such as ants and bees, that use polarized light to help them navigate. Reppert suspected that migrating monarchs, too, might use a polarization compass to locate the sun. If so, they should have the proper machinery—those precisely arranged simple eyes of the DRA.

To look for that geometry, one of Reppert's collaborators peered into the monarch's eyes using an electron microscope. And sure enough, he found it. In the picture he took, the microvilli from the simple eye's nine light-sensing cells form a perfect rectangle, aligned just so in neat perpendicular stacks. The pattern is every bit as beautiful, with its precise and purposeful order, as the monarch's colorful wings.

Reppert says this structure allows the butterflies to create in their brains a virtual grid-like map of the sky's polarization pattern. "And the nice thing about polarized light," Reppert adds, "is you don't have to see the sun, you just have to see a little bit of blue sky." So if the monarchs can in fact use polarized light as part of their sun compass, they could stay on track even under mostly cloudy skies, or when mountains obscured the sun itself.

On a windowsill in Reppert's office rests an elaborate sculpture, an intricate three-dimensional ceramic lattice. A similar piece adorns a shelf across the room. These sculptures are the work of Stan Hunter, who was inspired by the idea of a polarization compass. Hunter worked with Reppert and his collaborator Adriana Briscoe to create an exhibit called *Migration Grids*—the source of the two sculptures in Reppert's office.

Daylight streams in through Reppert's windows and filters through the clay lattices, casting delicate fringes of shadow that morph along with the sun's changing angle throughout the day. They call to mind, as they are meant to, the shifting patterns of polarized skylight—that fingerprint following the sun, invisible to us but commonplace to insects—that may guide the monarch's sun compass.

The picture of the monarch's DRA, with its precise polarization-sensitive organization, was intellectually enticing and aesthetically evocative. But Reppert still needed to show that polarized light could affect the orientation of a real, live, flying monarch. To test his theory, he returned to the field behind the Sheep Barn to tinker with the butterfly flight simulators. First he placed a polarizing filter—a thin film that polarizes light in a specific direction as it passes through—over the top of the barrel. This filter was designed to mimic the natural polarization of skylight at the zenith. He could then manipulate the filter and observe how the butterflies responded. Because the barrel of the simulator was small, and because he carried out experiments in the morning or afternoon when the sun was low in the sky, the butterflies could not see the sun itself.

In a video recording of one experiment, a tethered monarch is first shown flying under normal conditions, with no filter. It flaps its wings steadily, aiming southwest, seemingly oblivious to the fact that it's not going anywhere. Next, the polarizing filter is placed over the top of the barrel in such a way as to match the sky's current polarization. The butterfly continues to "fly" in the same direction, unfazed by the filter. But then things get interesting. The polarizing filter is rotated 90 degrees, changing the direction in which the light vibrates. Right on cue, the monarch suddenly veers in a new direction—spun 90 degrees from its original compass heading. Intent on its new course, it resumes its steady fluttering.

Next, the filter is rotated another 90 degrees, but this time a piece of clear plastic is placed over the top of the barrel. The plastic prevents ultraviolet light from entering the barrel. The light-sensing cells in the monarch's DRA are specifically sensitive to ultraviolet light. Without ultraviolet light, the butterfly's DRA is effectively blind—and the butterfly is therefore blind to polarization patterns. With the plastic over the barrel, the monarch is completely disoriented. It rotates this way and that, never settling on a direction. Finally, the plastic is removed, and the butterfly snaps back on course, neatly accommodating the second filter rotation.

The butterfly in the video wasn't exceptional. Reppert tested 13 monarchs, and 11 of them changed direction in response to the rotated filter. On average, they spun 90 degrees, corresponding to the 90-degree filter turn. With this result in hand, he was convinced that the monarch's internal compass needle is sensitive to polarized light. Reppert published his flight simulator results, along with the striking picture of the monarch's DRA simple eye, in *Current Biology* in 2004. His decisive title said it all: "Polarized Light Helps Monarch Butterflies Navigate."

But as confident as Reppert felt about the meaning of his results, the polarized light issue was not so cut and dry. In fact, Henrik Mouritsen, along with Barrie Frost and some new collaborators, were finding just the opposite. When Reppert's paper came out, they were in the midst of their own polarization experiments with the flight simulator. Their methods were very similar to Reppert's, but the Canadian group's setup allowed the monarchs a relatively narrower view of the sky. In their preliminary experiments, Mouritsen's group found that the monarchs—more than 100 of them—could not orient themselves using polarized light alone. Without a direct view of the sun, they steered themselves in random directions—with or without a polarizing filter. When the polarizing filter was rotated by 90 degrees, the butterflies, on average, did not respond.

In light of Reppert's paper, the Canadian group modified their apparatus to match the one Reppert was using, and repeated their experiments. But the contradiction persisted. Even with the same broader view of the sky that Reppert's monarchs had, the Canadian monarchs were completely indifferent to polarized light. For these monarchs, no sun meant no compass.

Besides barrel size, there was one other crucial difference between the two groups' experimental setups. Mouritsen's group noticed that even though the sun itself was invisible to the tethered monarchs, it created distinctive patterns of brightness on the inner walls of the simulators' barrels. They knew that many insects can use such patterns, called intensity gradients, to help them navigate. So to eliminate the patterns, they erected huge wooden sunshades, mounted on ladders, that cast shadows over the flight simulators. With these shades in place, they reasoned, the butterflies could see polarization patterns but not brightness patterns. When they removed the shades, to emulate Reppert's setup, they found that the monarchs regained their ability to steer southwest.

Perhaps, then, Reppert's monarchs were responding to intensity gradients rather than to polarized light. Reppert's group did not, after all, use sunshades. They did measure the brightness patterns within the barrel before and after they rotated the polarizing filter. Based on those measurements, they concluded that turning the filter didn't change the patterns. But Mouritsen wasn't concerned that filter rotation altered the patterns; he was concerned that there were patterns at all. He describes a distinct bright splash, shaped like a half-moon, where the sun reflects off the inside of the barrel. Could Reppert's butterflies have responded to that splash of light, rather than to subtle polarization patterns? Perhaps. Nonetheless, Reppert's video seems compelling: turn the filter, and the butterfly turns.

Mouritsen is not convinced. He invokes statistics to illustrate his sentiments. Reppert used just thirteen butterflies; Mouritsen's group used hundreds. Reppert counters that he was careful not to use indecisive butterflies—if a butterfly failed to fly in a consistent direction at the outset, he excluded it from the experiment. And so it goes: argument and counterargument, thrust and parry, *ad infinitum.*

As it turned out, these two groups weren't the first to wonder about the role polarized light might play in monarch orientation. After Reppert's paper was accepted for publication by *Current Biology*, he stumbled across an unexpected gem. In the early 1990s, unencumbered by the controversy that now bogs down the issue, a University of Pittsburgh Ph.D. student named Marty Hyatt had carried out his own series of polarization experiments. Using a primitive flight simulator of his own devising, Hyatt asked the same question Reppert and Mouritsen would ask more than a decade later. Like Reppert, Hyatt found evidence that polarized light could indeed guide the monarch's sun compass. "I thought he had a very compelling case," Reppert says. With a little laugh, he adds that in retrospect, his own paper merely confirms Hyatt's conclusions.

Does the sun compass respond to polarized light? Mouritsen's group says an emphatic no; Reppert's group says an equally emphatic yes. Science can't always provide the tidy answers we might like. It progresses in fits and starts, pedaling forward and then backward, as evidence gathers and scientists struggle to frame and interpret it.

Ultimately, Reppert says, the evidence is most important. "People, I think, need to look at the data and make their own decision," he says. "But as far as I'm concerned," he continues, "I'm convinced they use polarized light." He doesn't believe polarized light is the only input into the sun compass—or even the most important. "I think Mouritsen is right," he says, "that when they see the sun, that is overriding." Nonetheless, he maintains that the polarization-sensitive facets of the DRA are an important piece of the sun compass. "On cloudy days," he muses, "polarized light seems to me to be the best game in town."

Whether or not Reppert is correct, all the flight simulator experiments have provided intriguing clues about how the sun compass operates. But it's not just a sun compass; it's a time-compensated sun compass. So how does the time compensation work? To tackle this question, Reppert turned to his specialty: the circadian clock.

Clockwork

In confirming the monarch's time-compensated sun compass in 2003, Reppert's group found that by breaking the clock, they break the compass. No matter what time of day it was—in their heads or in reality—monarchs with stopped clocks steered a straight course for the sun. To Reppert, this meant that the circadian clock is vital; without it, the monarchs would never find their way to Michoacán. A monarch that stops short of the overwintering sites won't survive the winter, and even if it did it would find itself mateless in the spring. For a monarch, a functional clock is a matter of life and death. So how does this essential timepiece work?

Circadian clocks are nearly universal; virtually every organism on the planet—including animals, plants, and even some bacteria—has an internal timepiece of some kind. These clocks are an evolutionary consequence of living on a planet that rotates once every 24 hours. Each day, without fail, the sun will rise and then set; day and night are a given. Most living things have differing agendas for day and night. We diurnal humans are active when it's light, and rest when it's dark. Nocturnal mammals, such as hamsters, do the opposite. Many plants open their flowers during the day, and close them during the night. Every day, sunlight resets the clock, keeping it in sync with the Earth's rotation. But surprisingly, the rhythms continue even without the daily cycle of light and dark. For example, hamsters housed in total darkness still live on a roughly 24-hour cycle. The term "circadian" reflects this phenomenon; from the Latin *circa* and *dies*, it literally means "around a day."

These endogenous rhythms allow organisms to anticipate, rather than merely react to, the predictable events in their daily lives. Each morning, for instance, our circadian clocks prepare us for waking by adjusting our body temperature and the levels of certain hormones. When the sun comes up (or our alarm clocks go off), our bodies have already begun to help us wake up.

In monarchs, the circadian clock determines when an adult butterfly will emerge from its chrysalis. Normally this happens in the morning, after the sun comes up, but even in total darkness adult butterflies emerge whenever morning would have been. The clock may also dictate when the fall migration begins, by keeping track of day length. And in addition, as Reppert's experiments showed, the monarch's circadian clock directs the sun compass, by keeping track of the time of day and adjusting the compass needle accordingly. To understand how this process works, Reppert wanted to understand how the monarch's clock works. What are the gears, and how do they work together? How does the clock communicate with the compass?

Reppert's group began by hunting down the exact location of the circadian clock in the monarch butterfly brain. First, they pinned down the likely pieces of the clock, by looking for monarch proteins that resembled clock proteins from other insect species. Once they had found several such proteins, Ivo Sauman, Reppert's collaborator at the Czech Academy of Sciences, created molecular probes for each one. Each probe would stain its corresponding protein a different color. Using these probes, he stained thin slices of monarch brain and then looked to see what colors appeared, and where. And because this was, after all, a clock that they were looking for, they also wanted to know *when* the colors appeared. By comparing brain slices from monarchs killed at various times of day, they were able to search for brain regions that not only glowed with all the right colors, but also glowed in a rhythmic way over time.

This careful hunt led them to exactly four cells: two in each hemisphere of the brain, in a region called the *pars lateralis*. They had found the butterfly clock. This vital component of the time-compensated sun compass, without which the monarchs would never make it to Mexico, was contained within just four brain cells. These cells glowed with the colors corresponding to all the major gears of the clock. Each color ebbed and flowed in a daily cycle—even when the experiment was performed on butterflies housed in total darkness. It was a true circadian rhythm.

The staining experiments also revealed something unexpected, something Reppert found very intriguing. The probe for a clock protein called cryptochrome (CRY for short), which glowed red under fluorescent light, rhythmically lit up those two clock cells on either side of the brain. But in addition, on either side, a mysterious trail of red snaked out from those cells, tracing a distinct pathway to another brain region. "This pathway," Reppert says, "excited me greatly when I saw it."

As Reppert recounts the discovery, his tone changes. He had been rattling off neuroanatomical jargon while pointing to a cartoon of the monarch brain on the screen of his laptop; now he leans in and speaks more softly, as if he's letting me in on a juicy secret. Then his smile gives way to an almost gleeful laugh. Noting my baffled expression, he continues his explanation. "You may say, 'who cares?'" he says, nodding in my direction; "'why would you get so excited?'"

The reason Reppert was so excited about the CRY-stained pathway was that he could see exactly where it led. On each side of the brain, the trail traced a path from the two timekeeping cells to a part of the brain directly linked to the polarization-sensing DRA of the monarch's eye. In other words, it connected the circadian clock to what Reppert sees as part of the sun compass.

When he saw that, Reppert recalls, "all sorts of bells rang out in my head."

To confirm the clock-compass link, Sauman injected a special dye into the light-sensing cells of the DRA. This dye would pass from the eye cells into the brain cells they communicate with, leaving a visible trail. When he looked at brain slices from monarchs injected with the dye, he saw that the dye trail led straight to that CRY-stained pathway that originated at the circadian clock. Dye injected into non-DRA eye cells, on the other hand, didn't track to the CRY path. There seemed to be a strong, specific link between the monarch's circadian clock and the polarization-sensitive structures in its eyes. Could this be the underpinning of the time-compensated sun compass?

Reppert, along with several colleagues and collaborators, published these findings in *Neuron* in 2005. "We have do to more," Reppert cautions, "and we have to prove it." It's the typical guarded optimism of a careful scientist, but it's optimism just the same.

What about those contradictory polarized light experiments? Reppert and his group believe that the DRA provides sun compass information to the brain—that's the premise that makes his results so interesting. But what if the premise is wrong? Frost and Mouritsen's group don't agree with Reppert about the importance of polarized light to the sun compass. In fact, they found that monarchs could use their time-compensated sun compass even with paint covering their DRA, rendering them blind to polarized light. Nonetheless, based on his own findings, Reppert maintains that the DRA plays a role in telling monarchs where the sun is. To him, the apparent link between the DRA and the clock remains tantalizing. The glowing red CRY pathway seemed to unite the clock and the compass in the monarch butterfly's brain.

The ancestral clock

Beyond the promise of that glowing red trail, cryptochrome had yet more secrets to reveal. Now that Reppert had located the clock, he wanted to know what made it tick. He had identified several of its gears, including CRY, but he wanted to tease apart how they worked together in those four monarch brain cells to keep time.

"The way I look at this, and what fascinates me as a neurobiologist," Reppert says, "is trying to understand the molecular logic." And on a molecular level, he explains, "there are a number of ways you can build a clock."

Instead of studying in meticulous detail the circadian clocks of every living being, scientists focus on representatives of particular groups. For example, the mouse circadian clock is often used as a model for how mammalian clocks are built. Similarly, the fruit fly clock has long been a stand-in for insect clocks in general. Circadian biologists could safely assume that the monarch clock would resemble that of the fruit fly more than that of the mouse, because the monarch is more closely related to the fruit fly. The fruit fly is much easier and cheaper to study than the monarch; its long history as a so-called model organism means that there are many well-established tools and procedures for working with it. So it seemed like a reasonable, and practical, approximation.

In the fruit fly, as in most organisms, the clock resides in individual timekeeping cells. It works by manufacturing and then destroying certain proteins in a feedback loop that takes about 24 hours to complete. This feedback loop can sustain itself indefinitely, which is why the clock keeps working even in constant darkness. When the fly encounters daylight, though, a specialized protein in the timekeeping cell absorbs the light; it tells the clock that the sun is out by feeding into the loop. This specialized protein is CRY, the fruit fly version of the protein that illuminated the possible clock-compass connection. CRY is how sunlight sets the fruit fly's clock.

But Reppert wanted to figure out how the monarch's time-compensated sun compass works, so he couldn't rely on the fruit fly model—fruit flies don't use a sun compass, time-compensated or otherwise. He decided he needed to take a closer look at the monarch clockwork, to see how the butterfly clock works.

Because the fruit fly and the monarch are close evolutionary relatives, they share many of the same genes. Reppert's group had already found that each of the genes encoding the fruit fly clock's main gears has a counterpart in the butterfly clock, with a similar gene sequence. So far, it looked like the fruit fly clock was a good approximation of the monarch's. But that would soon change.

In the wake of the discovery of that suggestive CRY pathway in the monarch brain, Reppert's group had begun a series of experiments to uncover the molecular underpinnings of migration. While these studies weren't aimed specifically at the circadian clock, they yielded an unexpected insight into the clock's gears. Reppert wondered what, at the molecular level, distinguished non-migratory summer butterflies from migratory fall butterflies. Were there particular genes that were active in migrants on their single-minded southbound treks, but inactive in non-migrants on their desultory northbound hops? Or vice versa?

Back in the lab, postdoctoral researcher Haisun Zhu was removing hundreds of monarch brains and grinding them to mush. He made one pool of mush for northbound summer butterflies, and another for southbound fall butterflies. With the help of another lab, the pools of brain glop were analyzed to catalog all the genes that were active in each. They found about 10,000 unique genes, more than 400 of which were active to substantially different degrees in the two monarch populations. These genes, Reppert knew, held the secrets to why and how monarchs migrate—why a monarch hatched in May will go about the normal business of being a butterfly, while a monarch hatched in September will be drawn irresistibly toward Mexico.

Meanwhile, at the University of California, Irvine, Adriana Briscoe—one of Reppert's longtime collaborators—was looking through a similar catalog of mosquito genes when she noticed something bizarre. As expected, the mosquito had a CRY gene similar to that in the fruit fly. But unexpectedly, it also had a second CRY gene—one that looked much more like that of a mouse.

Just as in the fruit fly clock, the mouse clock keeps time using feedback loops. A number of clock proteins, which interact in an intricate network, are assembled and then destroyed in a cycle that takes about 24 hours to complete. Because the two clocks have been evolving independently for hundreds of millions of years, the mouse gears are different from the fruit fly gears. The mouse does have CRY genes of its own—two similar ones, in fact—which are only distantly related to the fly's CRY.

So what on Earth was a mouse-like CRY doing in a mosquito?

Briscoe called Reppert to tell him the weird news. Reppert remembers being surprised; "Really?" he recalls asking her. She suggested he check the newly minted monarch catalog for a similar gene.

"And we looked," says Reppert, "and lo and behold, there was a second cryptochrome"—one that bore a striking resemblance to the mouse version. "This," he adds emphatically, "had never been discovered." It was one of those truly serendipitous scientific moments, when chance and circumstance come together to produce an extraordinary finding.

"It was just a matter of luck," Zhu says of the discovery.

"We just kind of stumbled upon it," Amy Casselman adds.

Suddenly there were countless questions to be answered, countless experiments to be performed: What does it mean that the monarch and the mosquito have two distinct CRYs? What is the function of each? Does the mouse-like protein function the same way in the monarch that it does in the mouse? Are there more insects out there with both kinds of CRY? Reppert's group got right to work.

In the fruit fly, CRY is the messenger through which light resets the clock, to keep it in sync with the rising and setting sun. In the mouse, the CRYs play a very different role. The mouse proteins don't absorb light; they instead function as essential gears in the clockwork mechanism, the feedback loop that keeps 24-hour time.

For convenience, the fly-like version of the monarch gene was dubbed CRY1, and the mouse-like version CRY2. Reppert suspected that CRY1 would respond to light, as in the fruit fly, and CRY2 would be part of the feedback loop, as in the mouse. To verify this hunch, Zhu and Quan Yuan, another postdoctoral researcher in Reppert's lab, began to investigate how these proteins behaved.

In the first series of experiments they compared each protein to the light-absorbing fruit fly CRY. So for each protein they asked, can it sense and respond to light? When they shined light on the monarch CRY1—and that of the mosquito—the proteins responded strongly. In contrast, when they shined light on the monarch and mosquito CRY2 proteins, there was no response. In short, the monarch and mosquito CRY1s were behaving like fly CRY, and the corresponding CRY2s were not.

Next, the group tested each CRY for mouse-like function. So this time they asked, which proteins can function as a gear in the clock? To do so, they created an artificial clock-like system. Into this system they threw each protein, to see if it could integrate itself. And this time, the monarch and mosquito CRY1s failed the test, while their CRY2s passed. With the CRY1s, the clock wouldn't tick; with the CRY2s it kept time.

Taken together, all these experiments suggested that Reppert's hunch was correct. Function seemed to match form. The fly-like CRY1s seemed to behave as light receptors, just as in the fly. And the mouse-like CRY2s appeared to feed into the central clockwork, just as in the mouse.

In April of 2006, Reppert's group published these preliminary results in *Current Biology*, in a paper entitled "The two CRYs of the butterfly." Since then, they have continued to experiment with the butterfly's two CRYs, trying to confirm their disparate functions. Using an arsenal of new approaches, the group has been amassing more and more evidence to support what amounts to an astonishing discovery with wide-reaching implications.

Inspired by the monarch and the mosquito, Reppert and Briscoe wondered whether other insects might have a second CRY as well. To find out, Briscoe searched through the gene sequences of several insect species, looking for genes that resembled either the fly-like CRY1 or the mouse-like CRY2. What she found was that even among the insects—which were all previously assumed to resemble the fruit fly—there are several ways to build a clock.

First was the fruit fly, with just its lone, archetypal CRY1. Second was the monarch, joined by the mosquito, the Chinese oak silkmoth, and the commercial silkworm. All these insects had two CRYs—one that was fly-like, and one that was mouse-like. And finally, a third type of insect clock turned up, in the honeybee and the beetle. These bugs had the mouse-like CRY2 but not the fly-like CRY1. Parts of their circadian clockwork, it seemed, might be better typified by the mouse instead of the fruit fly.

In light of these insights, Reppert argues that the fruit fly is an inadequate model for insect circadian clocks. True, the fly is backed by a formidable edifice of tools and protocols, but among insects its clock is more the exception than the rule. Perhaps, Reppert believes, the insect clock would be better exemplified by the colorful monarch butterfly. Incorporating elements in common both with other insects and with mammals, the butterfly clock could help us better understand how clocks work and how they have evolved.

"It's really a new sort of frontier for clock studies," Reppert says of the evolutionary insights that CRY has made possible. He refers to the monarch's circadian clock, with its two CRYs, as an example of the "ancestral clock"—the kind of internal timepiece from which other clocks have evolved. In these clocks, one CRY mediates the resetting effects of light, while the other CRY is an essential gear in the clockwork. The other two kinds of clocks, which have either CRY1 or CRY2 but not both, likely represent evolutionary adaptations. Those with only CRY1—like the fruit fly—have developed some other gear to replace CRY2 in the clockwork. Those with only CRY2—like the bee, the beetle, and even the mouse—have developed other ways to sense light. In the mouse, for example, light enters the clock by way of the eyes.

In the migrating monarch, then, sunlight serves two indispensable purposes. It illuminates the clock, synchronizing it with the rising and setting sun. In this way, fall's abbreviated daylight most likely tells the butterfly it's time to head toward Mexico. And the sun also illuminates the sun compass, which works in tandem with the clock to keep the butterfly on course.

In Reppert's sleek, modern lab at the University of Massachusetts Medical School, sunlight streams in through an entire wall of windows. Full, natural light suffuses the room, casting its glow onto the shoulders of the researchers, onto the plastic monarchs tacked over desks, and onto the piles of papers arranged on a shelf beside the window. The papers bear elaborate figures, the results of the ongoing CRY experiments. Each figure sits atop a stack of its earlier drafts. They're shaping up, coming into sharper focus as holes in the data are incrementally filled in. The stacks are miniature scientific monuments, reverent testaments to the butterfly clock, built of painstaking work. They glimmer slightly in the sunlight, which quietly calibrates the clocks of scientists and butterflies alike.

By studying the circadian clock, Reppert and his colleagues are beginning to unravel some of the mysteries behind the monarch butterfly's spectacular yearly migration. And by studying the monarch butterfly, they have stumbled upon some unexpected insights into the molecular workings and evolutionary history of the circadian clock.

The ultimate road trip

In January, there are no monarchs in the Reppert lab. The field at the Worcester Foundation is hard-frozen under a dusting of snow, the hut empty but for disassembled simulators and empty soda bottles. And it's not just Reppert's lab that's monarchless. The whole vast red zone on Reppert's map is drained of monarchs for the winter. All of Canada, all of the United States, and most of Mexico are without their flitting orange-and-black residents. To see the monarchs for myself, I had to chase them down to that tiny yellow splotch on the map, on the face of the Transvolcanic Mountains in northeast Michoacán, Mexico.

The day after we visit the monarch sanctuary at El Rosario, we head over to another at Sierra Chincua. This one is smaller, less developed and thus less restrictive. There are no paved trails or rope cordons to keep us on track. On the backs of tiny, tired horses, we follow Tom Emmel up a convoluted trail. At the top, we dismount and hike a short distance to the pouting lip of a cliff. We sit with our lunches and our cameras, tipped out towards a gaping vista, row upon jutting row of Transvolcanic ridges fading into the atmosphere. The butterflies seem to celebrate the view, thousands of them twirling through the thin air like dust motes.

Emmel negotiates with a local guide to lead us down into the forest to the colonies themselves, where immense clusters of monarchs weigh down the branches of the oyamel pines. It's a steep descent across loose, jagged rocks that skitter under our boots. We thrust our arms out for balance as we ski inadvertently on pine needles. Down here, the monarchs are like fog, like when you descend through clouds in an airplane and everything is obscured by hovering water droplets. The hard, heavy sunlight makes the butterflies glitter and makes us pant; we dressed for winter and are shedding layer after layer as we hike.

And it's the sunlight, the unseasonable warmth, that draws the monarchs out of the trees in such mind-boggling numbers. Emmel remarks that in all the years he's been visiting the overwintering sites, he's never seen so many monarchs flying in January. Nature says they ought to stay in their cozy clusters. Their insect bellies are stuffed with fuel to last them the winter, but only if they remain huddled in the trees. Too much fluttering about will dwindle a winter monarch's reserves and likely hasten its demise. Not until late February or early March should they abandon their havens to mate and head north.

But this winter, the weather has other ideas. As we pause in a clearing to take pictures, Emmel spots a pair of mating monarchs. He is flabbergasted. "This should never happen in January," he says, as we all watch their violent, thrashing embrace. "They're sinning. On a Sunday morning!" He shakes his head. "The world is coming to an end."

For the mating butterflies, the world is indeed coming to an end. Once they've mated, they will leave the colony and head north into the Mexican desert. But there, because it's January, they will find no flowers to nectar from. Beyond that, in Texas, they would find no milkweed on which to lay their eggs.

The overwintering monarchs have always been vulnerable to the vagaries of the weather. A deep freeze can kill them by the hundreds of millions, leaving piles of dead monarchs Emmel likens to snow drifts, sometimes two or three feet deep. The forested microclimate of the overwintering grounds used to provide a buffer against the worst weather. But in recent years, farming and illegal logging have stripped much of the area bare. In the thinning forest, the colonies have become more susceptible to extreme weather.

Down among the clusters, in the deep shade of the forest, the air is cooler. Boughs fat with butterflies droop directly over our heads. The tree trunks are coated with a solid layer of butterflies, a quivering, deep orange mosaic. As I lie back on the dusty ground and peer straight up into the rustling clusters, I am reminded of the woman at El Rosario, for whom the sight was nothing short of a miracle. I want to find her, to tell her about cryptochrome and flight simulators and polarized light—not to disabuse her of her pure wonderment, but *because* of her pure wonderment. Hearing the story of the butterfly clock filled me with the same quiet awe that these magnificent clusters inspire. I want to share that awe with her; I want it to fill her, too. I want her to know that Reppert's science and her miracle aren't mutually exclusive: they are one and the same.

I am reminded, also, of Reppert talking about his son, who is a sculptor. Whenever Reppert gives a presentation on his research, he weaves in slides of his son's pieces. "Butterflies and art seem to go together," he explains simply. On a visceral level I agree with him. But why?

In some sense it's obvious; we are attracted to the bright patterning of the monarch's wings. It's an aesthetic sensibility. The monarch's grand migration, too, has its own aesthetic appeal. There's just something moving about a bedraggled butterfly arriving at its genetically predestined winter home after flying for hundreds or thousands of miles. It feels heroic, somehow—a mythic struggle against the elements, a testament to perseverance. Sandra Perez calls the migration "the ultimate road trip." The monarch's journey lends itself to human metaphor.

But the migrating monarch butterfly is not heroic. Its miniscule insect brain makes it a real pinhead, capable of acting upon genetic memory but not upon noble intention. And the migrating monarch butterfly is not mystical. Many aspects of its journey remain mysterious, but they do not transcend the knowable. As Reppert and countless other dedicated biologists have shown, the migration can—and eventually will—be explained on an ecological, cellular, and molecular level.

We are drawn to the obvious aesthetic of the monarch's colorful patterning, and to the subtler aesthetic of its cross-continental trek. But the emerging biological picture—the "spectacular biology" of the butterfly clock—has its own aesthetic appeal.

Besides, invoking miracles is just not the way Reppert operates; faced with overwhelming awe and wonderment, he invokes biology instead. Reppert describes himself as a purist, a believer in "science driven by curiosity." As with many scientists, it was curiosity that drew him to biology in the first place.

Every summer, Reppert raises cecropia moths, a ritual he began as a child growing up in the Midwest. Cecropia are extravagant at every stage in their life cycle. The caterpillar wears colorful rows of gaudy, spiky jewels; it spins an intricate cocoon the size of a large mouse. The brightly iridescent adult is the largest moth in North

America: with a wingspan of up to six inches, it dwarfs even the biggest monarchs. As Reppert describes the moths, he gestures at a painting of one that hangs on his office wall. He scurries off to fetch a glass-topped case, where an adult moth and several cocoons are pinned in place. These are beautiful insects; he simply likes to look at them.

But his attraction to cecropia is more than wing-deep. Reppert recalls one spring when he was nine years old. He had been rearing cecropia cocoons in a cage he built in his backyard, and a female moth had just emerged. He set his alarm for four in the morning, knowing that was when the male moths would be out on the wing. "The sun was just coming up, but barely," he says. "It was very eerie out, and the entire sky was filled with—like bats—the male cecropia, finding the female." Reppert understood that the female moths, like him, were responding to an alarm clock, in order to send out a properly-timed pheromone signal to attract the males while they were most receptive. "So that's really when the whole idea of this animal, and the environment, made sense to me in terms of timing," he says. "And I'm *sure* that's how I first got interested in clocks and biological timing."

Lincoln Brower, arguably the most influential living monarch biologist, echoes this kind of sentiment. For him, a large part of the monarch's aesthetic is its biology. He describes the overwintering sites with the usual reverence, saying, "I've been there forty or fifty times and it still amazes me; the experience is always fresh." But when I press him to explain what amazes him about the overwintering butterflies, his answer is unmistakably that of a biologist: "I was intellectually moved by them," he explains. "I looked at them and thought, 'Good God, the entire gene pool is sitting right here in front of me!'"

In any case, there's ample room within the science for wonder, for that ineffable aesthetic spark—whatever words we might use to describe it. To Reppert, the line between science and art blurs easily. "It's almost like a living sculpture," he says of the monarch: "a living piece of art that's gliding through the air."

Acknowledgments

I am deeply indebted to the generosity and patience of Steve Reppert and his lab members—in particular, Amy Casselman, Haisun Zhu, and Danielle Metterville. Reppert's contagious enthusiasm for all things insect cemented my budding interest in monarchs, and helped me understand what my thesis was about. I'd also like to thank Tom Emmel and Court Whelan, who led my trip to Michoacán to see the monarchs for the first time, reminding me why I loved my topic at a difficult time of year.

I'm grateful to Marcia Bartusiak, my tireless thesis advisor, who has been known to respond instantly to emails at the most improbable hours. Her guidance and feedback have been invaluable.

To the denizens of the lounge, my dearest fellow fivers, I literally could not have done this without you. In my darkest hours, you reminded me of the importance of South American geography, mirror neurons, and RNA polymerase. I have two parting words for you: "Domo: thesis!"

Last May, I wrote: "Everyone who has dealt with me this year has been extremely patient with my constant stress and thesis-obsession, but in that regard I am most thankful to Barbara and David Rice, Sera Moran, Arthur Hebert, and especially Dan Bauman." This May, I would like to write exactly the same thing. You all must have thought me crazy for doing this again. You were right.

Finally, I thank MIT's Kelly/Douglas Fund for financing my research in Mexico, and the Smith College Jean Fine Spahr Fellowship for making MIT possible for me.

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