

WINGS

ESSAYS ON INVERTEBRATE CONSERVATION



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Introduction:

Invertebrates and Global Warming

Scott Hoffman Black

Not long ago, as I was hiking along a roaring stream on my way up to Colorado's Red Cloud Peak, my mind wandered back to the summer of 1995. I had been hired by the Colorado Natural Heritage Program to help organize a search for the Uncompahgre fritillary (*Boloria improba acrocneuma*). With few known populations and multiple threats including sheep grazing, potential over-

collecting, and a prolonged drought that was thought to be drying out the habitat, this butterfly had recently been listed as an endangered species.

The Uncompahgre fritillary lives only in alpine meadows. Thought to have been broadly distributed near glacial margins during the last ice age, the butterfly is now confined to small patches of habitat above thirteen thou-



The San Juan Mountains of Colorado are home to the Uncompahgre fritillary (*Boloria improba acrocneuma*), one of many alpine insects that are vulnerable to climate destabilization. Warming climate may spell extinction for many of these species. Photograph by Scott Hoffman Black.

sand feet in the San Juan Mountains of southwestern Colorado, where cool and wet environments have persisted to the present.

On my recent trip, I was heading up to see how things had changed in the last twelve years. Although it was a little late in the year, I hoped to see a few late-season stragglers. The area looked much the same as it did in 1995. Snow willow (the Uncompahgre fritillary's larval hostplant) was still abundant. There were bumble bees, flies, and several species of butterflies including the arctic fritillary (*Boloria chariclea*), Uncompahgre's sister species.

I carefully made my way through the habitat hoping to spot an adult Uncompahgre. I thought about the complexities and uncertainties confronting us. Global warming will not lead to uniform change across the landscape. Some places will be hotter and drier while others may be wetter; in still others the weather may simply be more variable. It may affect plant communities and cause seasonal shifts that put species out of synchrony with their food sources.

After a fruitless search, I decided to hike the last few hundred feet to the ridge to take in the magnificent view. Just as I reached the very limit of the habitat, a familiar sight met my eyes. A faded and battered Uncompahgre fritillary fluttered across the trail to land on a rock a few feet away. I sat down next to the butterfly, noting that its life was near an end. I then looked up and realized that this species really has nowhere to go as the climate changes. It cannot live in the rock and ice at the top of the peak. I thought about what future generations will see when they come up this mountain. It might look the same,

but will it really be the same without a species that has resided here for thousands of years?

The Uncompahgre fritillary is not the only invertebrate facing a changing environment. In this issue of *Wings*, we explore multiple aspects of climate destabilization from the perspective of invertebrate conservation. Included are essays on how warming temperatures are already leading to bleaching corals and shifts in butterfly ranges. You will see that global warming may lead to the extinction of some butterflies and aquatic invertebrates. It may also lead to the loss of some marine worms that are an important food source for many birds and marine animals. In short, global warming is already having a profound impact on both terrestrial and marine ecosystems.

It is interesting to note that the first species thought to have been driven extinct by global climate change was a snail. Does it matter that one snail goes extinct or that the Uncompahgre fritillary may follow? There has been talk lately of taking action to protect some of the species that have been led to the brink of extinction by global warming. Some scientists have floated the idea of assisted migration (helping species move to habitat where they were never native). For most species this option is neither feasible nor wise. What we need to do is to take heroic efforts as a society to curb the impact of global warming. We must find the societal and political will to take the actions that are needed to curb this global threat.

To find out some changes that you can make as an individual, go to www.climatecrisis.net/takeaction/whatyoucando/index6.html.

Wetland Invertebrates: What Happens When the Pond Is Half-Empty?

John H. Matthews

In May 2003, I stuffed my car with camping and collecting equipment, said good-bye to my wife, and began a twelve-hundred-mile drive north from central Texas. On the front seat next to me sat a well-thumbed photocopy of a 1970 Ph.D. dissertation about dragonflies, written by a University of Toronto student named Robert Trottier. And the topmost page had a fuzzy photograph of a pond in Caledon, Ontario.

I was headed to Caledon to begin a multi-year study of the relationship be-

tween climate change and the aquatic macroinvertebrates found in small wetlands. Given the diversity and abundance of life they hold, these wetlands are both under-studied and beneath the radar of the public and policy makers. Most small wetlands are ephemeral aquatic habitats (that is, they dry up on a regular basis), but even “permanent” wetlands swing wildly in their annual water volume. Since many fish are intolerant of large shifts in volume, these fish-free habitats are typically rich in in-



Common green darners (*Anax junius*) are found at lakes, ponds, and wetlands across much of North America. Male, photographed in Texas by John C. Abbott.



When mating, the male dragonfly grasps the female behind her head, and she curls her abdomen around to accept sperm. Common green darners, photographed in Texas by Giff Beaton.

vertebrate diversity. Indeed, the top carnivore positions held by fish in larger bodies of water tend to be occupied by dragonfly or beetle larvae in such wetlands. But most of these wetlands are viewed as insignificant and marginal ecosystems, and many countries offer them little or no protection. In my long drive to Caledon I had time to ponder the question of just how sensitive these wetlands are to shifts in climate.

Climate change has been generally viewed through the lens of air temperature, a bias reinforced by the term “global warming.” However, in addition to air temperature, many aspects of climate such as wind speed, cloud cover, and relative humidity have been shifting over the past century. The majority

of the water in most small wetlands comes from precipitation. And in recent decades, the timing, form, and amount of precipitation have been changing. Less snow is falling. Globally, precipitation amounts are increasing and individual precipitation events on average are becoming more intense. But because air temperatures are also generally warmer, evaporation rates are higher. The effect is even stronger in arid and semi-arid regions, where, for the most part, precipitation is decreasing while evaporation rates are rising. As a result, many places—even those receiving more rain—are actually drier more of the time. To make the matter worse, the timing of precipitation is changing in many areas. As every gardener knows,

the timing of rain matters. Annual increases in mean precipitation are shifting at a monthly or seasonal scale in biologically significant ways. And all of these changes are likely to intensify in coming decades.

There are two major effects on small wetlands that could come from shifts in precipitation patterns. First, the timing or seasonality during which ephemeral wetlands hold water (their hydroperiod) is likely to alter. Such changes are important because many wetland invertebrates depend on a regular and predictable hydroperiod for their life cycle. If there's no water, they might need to speed up their rate of development or try to leave that wetland in search of another with a longer hydroperiod. If they can't disperse very well, they might have to survive harsh drying conditions, perhaps by entering a resting state. Or they might simply die, causing a local population to go extinct. For insects with aquatic larvae, such as stoneflies, diapause and death are the two most common responses to desiccation.

Second, water volume is also associated with temperature. Water is much harder to heat or cool than air because it has a lot of thermal mass. While large

bodies of water such as rivers and lakes tend to change volume (or temperature) slowly, even small changes in precipitation regime can radically alter the volume of small wetlands, and thus the temperature of their water. Less water volume means warmer water, since there is a smaller thermal mass. And more water means cooler water, because of the larger thermal mass.

Temperature matters to all organisms, especially invertebrates. Metabolism, development, activity level, reproduction rate, the ability to find prey or escape predation, and many other basic processes are influenced directly by temperature. Thus, changes in water volume that result in water temperature shifts should also alter behavior.

At least, these were my thoughts as I pulled into Caledon with Trottier's dissertation. Research into biological impacts from climate change faces some basic hurdles. Many of these studies are physiological, experimentally testing the tolerances of organisms to particular environmental variables like temperature or humidity. However, these studies have proven too difficult to generalize. Even closely related members of the same genus of butterfly or flower



Changes in water volume and temperature can impact the development and emergence of dragonfly larvae. Common green damselfly larva, photographed by John C. Abbott.

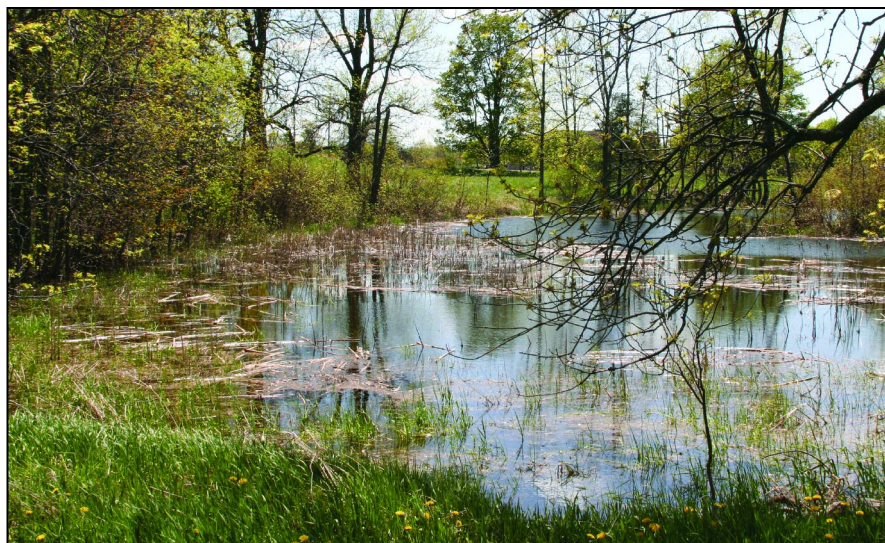
can have very different physiological responses to the same stimulus. Moreover, outside of the laboratory, multiple climate variables are changing simultaneously, and there is no guarantee that the selected variable in a laboratory will be very important in a natural setting. Historical studies that compare current behavior to an earlier period are an effective way to observe species' responses over time, which can then help us understand what further changes we can expect in coming decades.

Unfortunately, historical studies have been rather limited for invertebrates. Although insects make up the largest number of species on the planet (and have one of the largest biomasses), there are very few baseline datasets for studies on the impact of historical climate change. Which is why I had Trottier's dissertation with me in Caledon.

As a graduate student in the late

1960s, Trottier had no awareness of anthropogenic climate change. He was interested in untangling the developmental cycle of the common green darner (*Anax junius*), a species of dragonfly found from southern Canada to the Yucatan peninsula of Mexico whose larvae cannot survive outside of the small wetlands they favor. To explore their development, Trottier tracked emergence, the process of metamorphosis from larval stage to adult. When a green darner metamorphoses, the larva crawls from the water onto some projection such as a stick or cattail and then the adult emerges and flies away, leaving behind the empty exoskeleton.

Trottier hired a young field assistant named Mike McCormick, set up some fencing around the perimeter of a pond in Caledon as an emergence substrate, and waited. Trottier also brought some green darners into his Toronto labora-



Due to their small size and seasonally variable conditions, ponds and wetlands may be impacted by changes in both rainfall and temperature. This is the Caledon, Ontario, research site studied by the author. Photograph by John Matthews.



Many birds rely on adult aquatic insects for food. Tree swallows (*Tachycineta bicolor*), photographed in Quebec by Michel Bordeleau.

tory where he found that he could alter their rate of development by changing the temperature of their ambient water. Developmental rates were quite plastic, varying by factors of two to three over small temperature ranges.

I saw Trottier's emergence data from the late 1960s on the timing of emergence as a potential baseline for comparison, particularly since his research ended just before a period of relatively rapid climate change began. Starting around 1974, many climate variables began to shift swiftly worldwide. Moreover, Trottier had documented the importance of temperature on the development rate of green darners.

While in Caledon, I was especially lucky to meet the grown-up Mike McCormick, and he and his wife, Darleen, provided access to a pond that was very similar to the original site. With three young and excited field assistants of my own, I began four years of emergence and environmental monitoring at the McCormick pond. Following Trottier's method, we set up an emergence substrate. We found both that the timing

of emergence had changed since the 1960s, and that these changes were closely associated with decade-scale increases and decreases in precipitation. We believe that changes in thermal mass and hydroperiod in this wetland have significantly altered the timing of dragonfly emergence in Caledon over just the past thirty-five years.

How important are these results from a more general conservation perspective? Ontario is a relatively wet region in the northern temperate zone, and small shifts in dragonfly emergence may not be critical there. Except during drought years, there are abundant wetlands in eastern Canada of many sizes and thermal masses.

However, the implications of these results should be of serious concern in regions where surface water is more limited. In semi-arid regions, small ephemeral wetlands are often the most important and widespread type of freshwater habitat. For instance, across most of the Great Plains and the Great Basin of North America, small wetlands—often called prairie potholes or playa lakes at

the northern and southern ends of the Great Plains, respectively—are critical habitat and contain a different invertebrate fauna from nearby reservoirs and rivers. Many climate models suggest these regions will become drier in coming decades.

Therefore, in these regions changes in hydroperiod and thermal mass are likely to have a strong effect, and not just on dragonflies. Precipitation-driven changes in habitat are also likely to affect mayflies, stoneflies, caddisflies, dipterans (such as mosquitoes and midges), and many other groups. The impacts on these species will not be limited to freshwater taxa. Many bird species, for instance, specialize on the adult terrestrial stage of aquatic insect species. David Winkler of Cornell University believes that continental-scale changes in the timing of egg laying in tree swallows (*Tachycineta bicolor*) is an indirect effect of shifting climate on the emergence timing of aquatic dipterans, their primary prey. Given that many species are sensitive to the timing of behaviors in other species—think of the importance of the coordination between flowering time and a specialist pollinator—even minor changes can alter complex interspecies relationships. I fear that ephemeral small wetlands may be one of the types of habitats most endangered by climate change.

For the next decade, there are probably two broader lessons to keep in mind about global warming and freshwater invertebrates in small wetlands. First, few studies have focused on how climate change is altering wetlands, so more research should be conducted on this topic while more formal protection is enacted to reduce wetland destruc-

tion. In the United States, small wetlands are under growing pressure because recent judicial reviews of the Clean Water Act have eroded the ability of federal agencies to protect non-flowing freshwater systems.

Second, there are grounds for hope for small wetlands and the species they house if we can commit to their protection. These wetlands should be excellent candidates for protective legislation and active resource management. Particularly in regions projected to become drier in future decades, relatively small modifications to the shape and size of small wetlands can alter their surface-to-volume ratio, reducing the rate of evaporation and shifting the thermal regime. We need to give these species some more time to adapt during a period of intensifying climate change. In some cases, more small wetlands may need to be created at higher latitudes so that the ranges of species can move as their preferred climate “envelope” shifts spatially.

These wetlands are little worlds in themselves, full of life and activity. I find them beautiful and compelling. Our care for them and their inhabitants may tell us something about how prepared we are to help organisms in more complex habitats respond to our planet’s emerging new climate.

John Matthews is a freshwater climate change specialist with the World Wildlife Fund in Corvallis, Oregon. He continues to work on issues related to aquatic invertebrates, though occasionally he has to spend time on vertebrates as well. John thanks his Caledon field assistants, Nathan Burnett, Kieran Samuk, and Marie Riddell.

Bleached Out: Coral Reefs Under Stress

David Obura

Objects of great beauty in themselves, coral reefs are home to immeasurably diverse communities of marine life. Often described as “tropical forests of the sea,” or “gardens of paradise,” reefs support a tourism industry worth a billion dollars, and tens of millions of people living along tropical coasts are dependent directly on them for transport networks, building materials, fisheries, and the protection of coastlines.

Corals are closely related to sea anemones. The major difference is that many corals produce a cup-shaped skeleton of calcium carbonate, within which the anemone-like coral polyp lives. It is

this skeleton that gives stony (or scleractinian) corals their name. A few stony corals are solitary polyps that may reach ten inches (twenty-five centimeters) across, but the great majority are tiny polyps, usually less than an eighth of an inch (three millimeters) across, and live in vast, reef-building colonies.

Stony corals cannot successfully live on their own. For survival they rely on a symbiotic relationship with zooxanthellae, single-cell algae that live within the polyps. The relationship is clearly mutually beneficial. Indeed, it has evolved to the point of being effectively obligate in nature for the coral: the



Healthy corals form reefs of many different colors and shapes. This coral garden was photographed in Papua New Guinea by Tammy Peluso.



The purple areas of this *Pocillopora* coral are normal, while the pink and white areas are in successive stages of bleaching. The brown areas are dead. Photographed in the Mariana Islands by David Burdick; courtesy the National Oceanic and Atmospheric Administration.

two can survive apart in controlled laboratory conditions but in the real world, coral species that are normally symbiotic are incapable of maintaining themselves alone against competition and infection.

Through photosynthesis, zooxanthellae capture energy into chemical form, a large part of which they pass to the coral polyp. This provides the fuel for cellular functions within the polyp, including the creation of its calcium carbonate skeleton, which leads to the accretion of reef structures as new corals grow on the skeletons of previous generations. In return, the zooxanthellae are physically protected by living within the polyp, and the reef structure provides them with access to light, which they require to survive. They also require water temperatures greater than sixty-eight degrees Fahrenheit (twenty

degrees Celsius), so reefs are almost exclusively restricted to tropical seas less than 150 feet (50 meters) deep. The partnership between corals and zooxanthellae is one of the most successful on the planet; this relationship has existed for more than four hundred million years and the resulting reefs are the only biogenic structures visible from space.

Over the years, a picture has developed of coral reefs as highly sensitive networks of species in a delicate equilibrium. Cold temperatures have long been known to be inimical to reef survival, but in the 1970s evidence accumulated that showed corals have upper temperature and light limits as well as lower limits. By the 1980s, scientists were witnessing large-scale “bleaching” and mortality of corals believed related to warming seas associated with increasing levels of greenhouse gases in

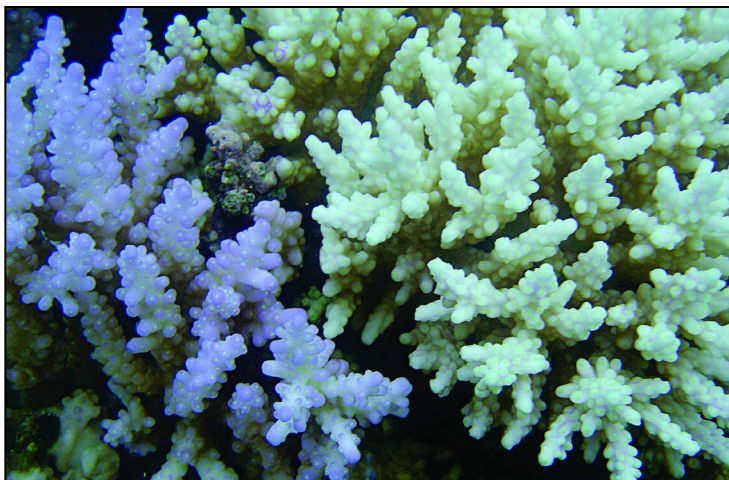
the atmosphere and perturbation of ocean-atmosphere oscillations such as the El Niño and La Niña cycles. Since that time, bleaching and mortality have increased rapidly.

It is now widely accepted among coral reef scientists that coral bleaching represents a last-ditch attempt by corals and zooxanthellae to resist stressful conditions. A wide range of stress causes them to separate, and the departure of the pigmented zooxanthellae from the coral tissue leaves the tissue transparent, revealing the bright white skeleton beneath. Under not-too-stressful conditions, the partners can often rejoin and continue growing; however, when conditions are too severe, bleaching is usually followed by mortality.

Excessive temperature and light intensities are the main causes of stress in the polyp-zooxanthellae symbiosis, and these two factors are increasing globally. Background levels of both are rising,

and peak fluctuations are being pushed higher than ever. Corals in all regions appear to be adapted to a late-summer peak of temperature and light when the sun is at its local zenith. However, any increment above seasonal norms pushes corals and zooxanthellae over their adaptive limit—and around the world temperature and/or light are beginning to exceed their historic summertime maxima. In 1998 alone, during the hottest year on record, coinciding with an El Niño peak in the Pacific and a similar climate peak in the Indian Ocean, 16 percent of the world's reefs were judged to be severely degraded.

The implications of continuing stress are dire for coral reefs. Although few species on a reef rely directly on stony corals for food or energy, the structure that corals provide enables the rest of the reef community to exist. The decline in coral diversity and cover on some reefs has resulted in lower diver-



Completely bleached corals are white; as they bleach they can take on fluorescent hues of purple, blue, green, or yellow. *Acropora* coral, photographed in the Mariana Islands by David Burdick; courtesy the National Oceanic and Atmospheric Administration.

sity and abundance of obligate associates of coral, those crustaceans and fish that live in spaces among branching corals, or fish that feed only on corals. If coral growth does not resume, the framework of the reef itself erodes, resulting in still lower diversity and abundance of fish, including many fisheries species of economic importance. In the Galapagos, where only small reefs ever build up, near-total death of corals in the El Niño of 1983 resulted in complete erosion of some local reef frameworks within the next twenty years.

Quantifying the potential loss of biodiversity from declining reef health is probably impossible. What would it mean if the area of healthy reefs declines to less than 10 percent of what it was a few decades ago? What is the likelihood of coral species going extinct?

The majority of coral reef scientists, managers, and enthusiasts, including the scientists on the United Nation's Intergovernmental Panel on Climate Change and the team that put together last year's Stern Review for the British government, believe that coral reef decline is a harbinger of decline in other ecosystems. Others who minimize the significance of coral reef declines point to the coral species that bounce back quickly after bleaching. These species, however, are mainly widespread generalists and not representative of all species on a reef, much as weeds and cockroaches are not representative of all plants or insects. Their ability to survive changing conditions masks the impact of such change on global coral diversity.

Of course no one can precisely predict the future for corals, but some outcomes are more likely than others. The climate-change debate is fueling new re-

search on coral and zooxanthellae evolution and physiology as well as reef dynamics, and it is clear that with two partners interacting, each with their own genomes, there are levels of adaptation and acclimation available to corals that we don't yet understand. Coral reef scientists are split between those who have measured very limited capacity for adaptation, and those who offer evidence for considerable capacity for adaptation.

In my view there will be many surprises, but it is hard to imagine that an ecosystem knocked down to just 10 percent of its historic extent by conditions that are predicted to become increasingly hostile, can have much chance of functional or widespread survival. Perhaps a few locations will retain functional coral reefs, and in fifty years we'll have to travel to South Africa or Japan to see the corals that make it farther from the equator as seas continue to warm. People may debate the details of coral declines but, for those who depend on coral reefs to earn enough money to support their families, it is not fair to say "no problem, no action needed," when we really don't know. There are many challenges that need our attention and that will benefit from a precautionary rather than a laissez-faire approach to climate change.

David Obura coordinates CORDIO East Africa, supporting activities in mainland Africa and the island states, including research, monitoring, and capacity building of coral reefs and coastal ecosystems. He has studied sediment stress and coral bleaching and life-history strategies, and has a primary research interest in climate change and the resilience of coral reefs.

Beer for Butterflies: Tracking Global Warming

Matthew L. Forister

The cabbage white butterfly (*Pieris rapae*) is so common and plain as to be of little interest to most butterfly enthusiasts. However, under certain conditions a cabbage white butterfly can be cashed in for a pitcher of beer. For more than thirty years, Dr. Art Shapiro of the University of California, Davis, has held a “Beer for a Butterfly” contest. A pitcher of beer goes to the person who nets the first cabbage white within California’s Sacramento, Solano, or Yolo counties on or after the first of the New Year. Since he has the ability to think like a butterfly, Dr. Shapiro usually wins. I tried, but never came close.

Around the turn of this century, as I was pursuing my graduate studies in

Dr. Shapiro’s lab, biologists were coming to a consensus that contemporary changes in our climate were having equally contemporary and dramatic changes on the plants and animals around us. For butterflies, much of the discussion was coming from northern Europe (England in particular), while we knew relatively little about the same phenomena at lower latitudes. This geographical disparity in our knowledge inspired us to examine the results from the “Beer for a Butterfly” contest. We found that the beer had been handed out earlier and earlier over the course of the previous three decades. In fact, the first cabbage white of the year was now appearing on average almost three



The cabbage white (*Pieris rapae*) is a European species naturalized in North America. Because of warming temperatures it now appears nearly three weeks earlier in the spring in some areas. Photographed in California by Henk Wallays.

weeks earlier, as were many of its fellow butterflies in the same region. These changes appeared to be related to warming and drying climatic conditions in the region.

Results like these from the cabbage white and its neighbors are all too common. Similar effects are turning up on every continent and with many different kinds of creatures.

Of species' varied responses to climate change that have been observed, shifts in geographic range and in the timing of life-history events (phenology) are of fundamental importance. Both kinds of changes follow from the fact that organisms depend on cues from their environment to determine when, where, and how to live out their lives. When conditions become warmer or drier (or colder or wetter), the environmental cues change and the biology of plants and animals may or may not change in response. It has become very clear (at least in temperate regions) that the phenology of butterflies is changing in predictable ways. In particular, the date when the first butterfly of many species is observed is coming earlier in the season.

Why does this happen? In regions with strongly seasonal climates, most butterflies spend at least part of the year in a dormant phase. This part of the year is often winter but in some cases, it's the heat of summer. Butterflies have a variety of ways of spending these dormant times: as different life-history stages and in different states of inactivity. For many butterflies, entry into dormancy is controlled by photoperiod (day length), and may or may not be influenced by temperature, while emergence from dormancy is largely tem-

perature controlled. Consider a butterfly that spends the winter as a caterpillar in arrested development. In the heart of winter, a succession of cold days causes the caterpillar to "break" dormancy and resume normal metabolic activity in preparation for spring. After that, subsequent growth and emergence may be dramatically affected by temperature: with a very warm spring, the caterpillars will grow more rapidly and the first adult butterflies will be seen earlier than in a year with a cold spring.

The other side of the coin is movement in space. Studies by scientists, including Camille Parmesan of the University of Texas and Jane Hill of the University of York, have shown that butterflies across Europe are shifting northward. In particular, a study of thirty-five non-migratory species found that, during the twentieth century, the ranges of nearly two-thirds of the species expanded northward by between 35 and 240 kilometers (22 and 150 miles). In some but not all cases, the southern edge of the range has also shifted northward.

An instructive example of similar movement comes from the western United States, and the work of Lisa Crozier of the National Oceanic and Atmospheric Administration. The sacheem skipper (*Atalopedes campestris*) has recently expanded the northern edge of its range from northern California to southern Washington. Through experiments in which caterpillars were exposed to a range of environmental conditions, Crozier was able to show that winter temperatures were the primary factor affecting the recent expansion. Pacific Northwest winters warmed by roughly three degrees Celsius (five and a half degrees Fahrenheit) in the second



The Sachem skipper (*Atalopedes campestris*) is found across the United States. On the West Coast its range has recently expanded northward into Washington state. Photographed in Virginia by Preston Scott Justis.

half of the twentieth century. Before the 1990s, winter temperatures in Washington were generally below a critical survival threshold for overwintering caterpillars; the threshold appeared to be average January minimum temperatures of minus four degrees Celsius (twenty-five degrees Fahrenheit). Once temperatures on average warmed above that point in the 1990s, the skipper was able to rapidly expand its range and is now a regular member of the Washington fauna.

A comparable phenomenon is the upslope movement of butterflies on mountains in response to warming conditions. In France, populations of a montane butterfly, the Apollo (*Parnassius apollo*), have gone extinct at lower elevations but, as described by Henri Descimon at the Université de Provence, in Marseille, they persist on plateaus at higher elevations. Where the lower-elevation populations are close to

suitable higher-elevation habitat, butterflies colonize the higher locations and establish new, viable populations. Robert Wilson of Madrid's Universidad Rey Juan Carlos reports similar behavior among numerous species in the mountains of central Spain.

So what's the problem with all this shifting around in space and time? For changes in space, the consequences may be painfully obvious. Montane populations can be pushed only so far upslope or poleward along a mountain chain: if warming continues, they may run out of mountain. The consequences of shifting in time are more subtle. The life cycles of many butterflies, particularly those with a single spring generation, are tightly timed to the phenology of their hostplants, the ones that the caterpillars depend on for food. Caterpillars may, for example, need to eat newly unfolded leaves, which are not only tender but also relatively free of the

toxins that accumulate as the leaf develops. If the butterfly's flight period is shifted either forward or backward, the adults may lay eggs but caterpillars will not find optimal foliage. It is also possible that the phenology of plants may change, but there is no particular reason to think that a shift in plant phenology will perfectly match a shift in butterfly phenology. Of course, climate change does not result in uniform warming. Many areas are receiving increased winter precipitation, which may delay development or even increase mortality through mold or disease; even if not killed outright, stressed larvae become less healthy adults.

If changes in range and phenology can lead to such problems, why don't organisms adapt to changing conditions and just stay put? After all, it is clear that butterflies have adapted to almost all manner of environments because we find them in the hottest deserts and on the highest mountains. Although the fact is that we know relatively little about the evolutionary responses of butterflies to climate change, examples are accumulating of one intriguing possibility: dispersal facilitated by adaptation. Populations at northern range boundaries may evolve greater dispersal ability (in response to newly available habitat), and, in the case of the brown argus (*Aricia agestis*), populations at a northern range boundary have colonized a novel hostplant, which subsequently facilitated range expansion, as described by Chris Thomas at the University of Leeds.

But what if there is nowhere to go? Is adapting to new conditions possible? The answer is certainly yes: we know of few true constraints on the evo-

lutionary process, but there are daunting issues of chance and time that all adapting populations face. For species with nowhere to go it seems likely that many will simply go locally extinct, including not only species on mountains—such as the Apollo butterflies trapped on warming plateaus—but also species in extremely localized or fragmented habitats.

Given the possibility of extinction in some cases, and phenological or spatial shifts in others, it's interesting to consider what your favorite butterfly community, in your backyard or local park, will look like in ten, twenty, or fifty years. It is quite possible that you will see one or two species that you have never seen before as they colonize from lower latitudes, and you might even spot a few tropical gems. It's equally possible that some species may be gone, either locally or globally, and that new ecological interactions may arise as plant and predator communities are also shifting around the butterflies. Outcomes will also depend on many factors not related to climate change, such as regional habitat destruction. In any event, the coming decades may be both intriguing and disheartening for observers of butterflies. Perhaps we should all have a "Beer for a Butterfly" contest, and raise a glass or two for the butterflies as they come and go in space and time.

Matthew Forister is a research assistant professor in the Department of Natural Resources and Environmental Science at the University of Nevada, Reno. His research involves the ecology and evolution of herbivorous insects, particularly issues of speciation and ecological genetics in butterflies.

For Marine Worms, Timing Is Everything

Andrew Lawrence

Let me begin by asking you to remove your watch, close your calendar, turn off your TV or radio, throw away your newspaper, and not speak to anyone. How long do you think that it would be before you lost track of time—the precise time of day, day of the week, or month of the year? And, if you were asked to keep track of time, how might you try to do this?

What if I said that you have the chance to meet the man or woman of your dreams at 7:00 in the evening of October nineteenth and that, if you meet, you will enjoy a night of passion leading to the birth of your only child? Do you think that you would be able to make the meeting? And, if I said that

you will die the next day, do you think that your genes would have been passed on to the next generation?

This is the challenge facing many invertebrates. Lucky then for the islanders of Samoa and Fiji that the palolo worm has managed to solve this puzzle. Each year, millions of worms release their epitokes, their rear sections full of sperm or eggs, which swarm at the sea surface to reproduce. The islanders have been able to predict the date and time of day of this phenomenon for centuries. At dawn on the day before and then on the actual day of the moon's last quarter in October or November, people row or wade out to sea with nets ready to catch the animals for the brief



During their annual swarm, palolo worms (*Palola siciliensis*) release epitokes, rear sections filled with eggs or sperm. The male epitokes are tan, those of females a darker gray-green. Photographed in American Samoa by Stassia Samuels; courtesy the National Park Service.

period that they are available. The palolos are considered a delicacy and eaten raw or cooked, and their arrival is often followed by festivals.

The palolo worm is one of the most dramatic examples of an animal that coordinates its reproductive cycle to lunar periodicity. However, spawning is only the final stage in a complex process of gamete (eggs or sperm) development and maturation, and in order for the worms to be able to spawn, the gametes have to be ready at the appropriate time. This too requires precise synchronization.

The most commonly used cues to regulate breeding are environmental: photoperiod and temperature. Of these, photoperiod (length of day) is the most accurate predictor of time of year and it is often used to entrain an animal's in-

ternal clock mechanism, which in turn controls the animal's annual cycle of activity or physiological processes (biorhythm). Temperature is a secondary control. While it also follows seasonal cycles, it can show significant variation on a yearly basis and may cause onset of certain phases of development at inappropriate times if it is used as the main cue.

Cueing to environmental cycles in order to synchronize reproduction is widespread in invertebrates, but some of the best examples are seen in the marine worms in the class Polychaeta.

Ragworms (genus *Nereis*; also called sandworms or clamworms in North America) are widespread in intertidal areas across the Northern Hemisphere. Up to twelve inches (thirty centimeters) long, they are found mostly in muddy



Intertidal mudflats may appear featureless and barren, but under the surface is a rich community of invertebrates waiting for the returning tide. England's Humber Estuary, photographed by Alan Clements.



Ragworms in the genus *Nereis* are agile predators when the tide covers their mudflats. Photographed in the North Sea by Edgar Donkervliet.

estuarine areas and may live for one to three years in temperate waters. When the tide goes out they retreat to U- or J-shaped burrows in the sand or mud. During high tide they emerge from their burrows as active, fast-swimming predators.

Ragworms are among the most important food sources for shorebirds and are preferred prey in Britain for birds such as dunlin, bar-tailed godwit, grey plover, and redshank. With burrow densities that may exceed several hundred per square yard, ragworms are a huge food resource, and consequently some estuaries are of national or international importance as migratory stopovers for birds. The Humber Estuary, for example, on the east coast of England, is one of Europe's key sites for wintering wildfowl and may host more than 175,000 birds. Its importance is recognized worldwide.

Ragworms are different from many other polychaetes in that they are semelparous—that is, breeding only once, after which the adult dies. Synchronizing the timing of reproduction is therefore essential and must be tightly con-

trolled, not only within the individual but also across the population.

The two most important factors controlling the development of eggs and sperm in ragworms are water temperature and photoperiod. In the king ragworm (*Nereis virens*), for example, egg development is initiated by the switch to short winter days—a day length of eight hours is essential to promote egg growth—but it is temperature that controls the speed of egg development. Low temperatures speed up development so that eggs starting to develop later in the winter grow faster at the lower temperatures they experience and catch up to those eggs that began development during the milder conditions earlier in the season. All eggs are ready for spawning in early spring.

Temperature has also been linked with spawning. For example, the ragworm *Nereis diversicolor* spawns in the spring after a period of low winter temperatures. In this species it seems that the rise in temperature from winter to early spring is highly important in

aiding the synchronization of gamete maturation and spawning. Further synchrony is imposed as mature animals release their gametes only with the spring tides, which occur on the semi-lunar cycle of 14.8 days and coincide with the full and new phases of the moon.

Scaleworms (genus *Harmothoe*) are another group of polychaete worms that utilize photoperiod and water temperature to synchronize reproduction. Like ragworms, they are widely distributed across the Northern Hemisphere and are an important food source for shorebirds, but they differ from ragworms in behavior, habitat, and life cycle. They are sit-and-wait predators of rocky shores, using cryptic coloration to hide in crevices or under stones or seaweed holdfasts, and are iteroparous, which means they reproduce once a year and may live for several years.

One species, *Harmothoe imbricata*, actually produces two batches of eggs each year, with the spawning of these occurring just weeks apart. The process begins in autumn when the first batch of eggs grows during the winter before being spawned in March. After this, the second batch of eggs develops rapidly and is spawned approximately three weeks later. Spawning is linked to calendar date and *H. imbricata* exhibits an annual reproductive cycle in which photoperiod sets the clock. The animals must be exposed to at least six weeks of continuous short days (thirteen hours or less of daylight) for successful egg development. Falling temperatures during this period also help to synchronize gamete progression to maturity. A final rapid growth phase is accelerated by low temperatures combined with longer day lengths as winter transitions to spring,

but only in those animals that have experienced at least fifty short days.

Scaleworms and ragworms, along with many other marine creatures, rely on a delicate balance of day length and temperature to control breeding. If one of these two environmental cues fails them, the worms may not be able to breed successfully. If an individual misses the spawning period, its individual genes may be lost from the population forever. If a population misses the spawning period, then the consequences will be more severe, not just for the worms themselves but also for the other animals that are reliant on them as a seasonal food source. Global warming makes this more than just a possibility. The United Nations' Intergovernmental Panel on Climate Change predicts higher surface temperatures, with the change 50 percent higher during winter in northern temperate regions than elsewhere, so it is likely that the relationship between photoperiod and temperature will be broken or fall out of phase.

For the species discussed here, the impact of climate change could be dramatic. The photoperiod cues will remain the same, so gamete development will be initiated and spawning will occur at the same time, but higher winter temperatures will slow the rate of development, leading to a significant reduction in the number and quality of gametes ready to spawn. Dissynchronous spawning between individuals has been seen in populations of *Nereis diversicolor* maintained in constant high temperatures. It may also lead to the time of spawning becoming uncoupled from the best time of year for larval survival. While this may not ultimately lead to

species extinctions, it could lead to the local extinction of some populations or the significant collapse of populations from some areas. Their survival will depend on the speed at which they can adapt to climate change.

Recent events in the seas around northwest Europe have shown that changes in environmental conditions during the winter can have significant impacts on marine invertebrate reproduction. Ecological responses to the climatic effects of the North Atlantic Oscillation have included changes in the timing of reproduction, population dynamics, abundance, and spatial distribution of marine invertebrates. In addition, unseasonable climatic events in the Baltic Sea have led to high losses of shearwaters due to a collapse in their food supplies.

The structure and function of marine ecosystems are intimately linked to the atmosphere, and the impact of climate change on these and other in-

vertebrates is likely to go beyond just the individual species. Because polychaetes are one of the most important components of the estuarine sediment community, loss of these animals may have a significant impact on the ecology of these systems. For some estuaries, any significant loss of invertebrate biomass could result in the loss of bird populations.

So finally, going back to your big night on October nineteenth, would you have made the meeting? Do you think that you would have noticed that this is the night of the third quarter of the moon in North America? I suspect that most of us would miss the date.

Andrew Lawrence has been studying marine worms and impacts of climate change for more than twenty years. He is a senior lecturer in marine ecology at the University of Hull, a couple of miles from the north shore of the Humber Estuary.



Invertebrates of intertidal areas provide a vital food resource for migrating or overwintering shorebirds. Photographed at the Humber Estuary, England, by Paul Glendell; courtesy Natural England.

Impacts of Global Warming on Pollinators

David Inouye

The global climate is changing. Although many of the finer details have yet to be revealed, the overall picture is one that portends trials and changes for invertebrate species generally and for pollinators specifically. Pollinators will face multiple challenges to their survival—many of them have complex life cycles that include dependence on different resources at different stages of growth, some have life spans of multiple years, and for others migration is a factor as well. Pollinators seem most likely to respond to a warming environment in two ways, through changes in phenology (the timing of life-cycle events), and through changes in their geographic distribution.

Phenology of both pollinators and the plants on which they feed is an important ecological factor that is changing in response to global, regional, and local climate changes. Key phenological events in pollination, including pollinator emergence or arrival and timing of flowering plants, generally appear to be happening earlier than in previous years in temperate regions of the world. Some of the clearest examples come from Britain. Data from the United Kingdom's Butterfly Monitoring Scheme show that the first appearances of most butterflies have advanced in the last two decades. These changes were strongly related to earlier peak appearances and, for multi-brooded species, longer flight periods. Models using these data suggest that climate warming on the order of

one degree Celsius (one and three-quarters degrees Fahrenheit) could advance first and peak appearance of most butterflies by two to ten days. This sort of change is not limited to butterflies. Although they are not pollinators, Britain's dragonflies and damselflies have been emerging about three and one-third days earlier for every degree Celsius of warming in temperature since 1960.

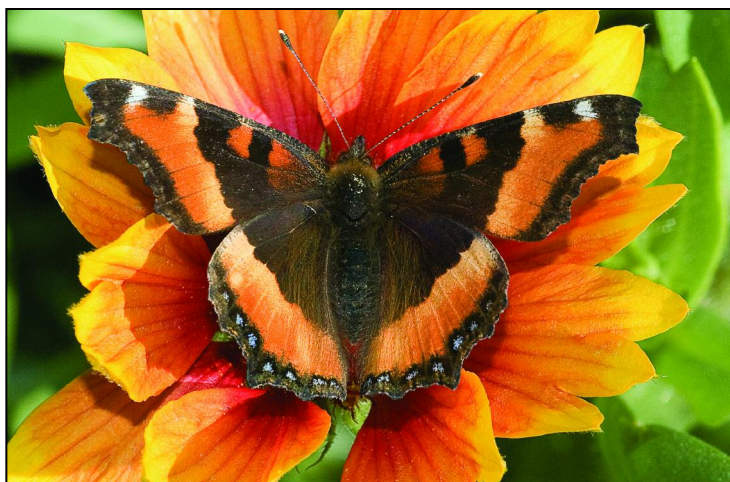
It also appears that the general arrival of spring has advanced in recent decades. Where detailed studies have been conducted on more local scales, earlier flowering is a common pattern for many species. A danger for pollinators comes from the loss of synchrony between their life cycles and those of the plants upon which they depend, either as hostplants or nectar and pollen resources.

My own research has been focused primarily on montane and alpine environments, particularly in Colorado, where I have worked for almost four decades at the Rocky Mountain Biological Laboratory. Here the emergence of Milbert's tortoiseshell (*Nymphalis milberti*), a butterfly that overwinters as an adult, has not been changing in concert with the flowering of early spring wildflowers, suggesting a loss of synchrony between their need for nectar and the availability of their customary floral resources. If this pattern turns out to be more widespread—if overwintering bumble bee queens or emerging solitary bees, beetles, or flies respond differently

than do spring wildflowers to changes in environmental cues (such as snow-melt dates and warming soil temperatures in temperate habitats)—it raises the possibility that changes to many historical plant-pollinator relationships are on the way.

A second prediction of the consequences of global warming is that some species will move their ranges to higher latitudes in the Northern Hemisphere or to higher altitudes in mountains. There is now evidence that some species of butterflies have already undergone such latitudinal changes, which matches the observation that some species of birds, fish, other insects, and plants have also expanded their latitudinal distributions. It would be surprising if other pollinators don't also respond to warming temperatures by moving toward the poles; there is already evidence available of bumble bees moving to higher mountain elevations.

One ongoing research project at the Rocky Mountain Biological Laboratory is an investigation of potential shifts in the altitudinal distribution of bumble bee (*Bombus*) species. In 1974 and 1975 Graham Pyke and I were graduate students at the Laboratory and both of us looked at the distribution of these bumble bees along altitudinal transects that spanned up to about 1,500 vertical feet (460 meters). The bees typically sorted out by a combination of proboscis length (short, medium, long) and altitude (high, medium, low). Consistent with the predictions for global warming, we have anecdotal evidence that species in this habitat are moving their ranges up in altitude. This summer we brought Dr. Pyke back to the Laboratory from Australia, where he now works, to help relocate his original transects from 1974. The students who then re-surveyed the transects last summer observed at least one of the bumble bee



Global warming is changing the timing of flower bloom and butterfly emergence, in some cases breaking synchrony between species. Milbert's tortoiseshell (*Nymphalis milberti*), photographed in Wisconsin by Mike Reese.

species about fifteen hundred feet higher than we had reason to expect to find it. The results of our recent census will provide both insight into any significant changes in distribution and another baseline for future studies.

Pollinators are dependent on plant species for nectar and pollen as sources of carbohydrate and protein, so it makes sense to consider how their interactions with plants may be affected by climate change. In some cases these are very specific relationships, with insects visiting only a single species of plant, or perhaps a group of related species, while other pollinators may be much more catholic in their diets. Perhaps the former strategy is the one most at risk under scenarios of climate change, for if the one species of plant a pollinator depends on shifts its distribution, or if its abundance decreases, the pollinator would have to duplicate the range shift or face a certain decline. Pollinators dependent on a suite of flowering plant species may

also face problems if gaps develop in the temporal sequence of resources they need. For example, bumble bee colonies are started early in the spring by queens emerging from overwintering under ground, but new reproductives aren't produced until the end of the summer, so a whole series of plant species must be available to sustain this long period of colony development.

In addition to changes caused by increasing global temperatures, the effects of increasing carbon dioxide could have implications for pollinators. In an experimental study in Britain, elevated carbon dioxide levels had an effect on flowering phenology and nectar production of some butterfly hostplants. In another experimental study, a change of food-plant preference was found for caterpillars under elevated carbon dioxide, and development took longer with increasing levels of carbon dioxide.

Yet another prediction of some climate-change scenarios is that there will



Pollinators are key components of terrestrial ecosystems, yet little research has been done on the impacts of global warming on bees, flies, and beetles. A bee fly on valerian, photographed in Colorado by David Inouye.

be increased variability in precipitation. At Stanford University's Jasper Ridge Biological Station, a nearly four-decade-long study of bay checkerspot butterflies (*Euphydryas editha bayensis*) found evidence that such variability may have amplified population fluctuations, leading to their local extinction. Modeling studies also suggest that rapid extinction could result from precipitation-amplified fluctuations in butterfly populations. Precipitation is also important for both the abundance of flowering and the abundance of nectar; in drought years plants may lose flower buds and the flowers that are produced may not produce nectar.

To date, butterflies have been the focus of most climate-change and pollinator research for a variety of reasons. They are easy to observe, there are often good historical records of distribution and abundance, and they seem to resonate with the public more than many other invertebrate species. But they are not necessarily representative of all pollinators; it is likely that many less mobile invertebrate species could face even greater challenges in responding to future changes in temperature, precipitation, and phenology.

The recent report on the status of pollinators in North America sponsored by the National Research Council pointed out that little is known about the ecology, the population biology, or even the distribution of most pollinators. This lack of information hampers both our ability to forecast the changes that are undoubtedly ongoing and our ability to plan for conservation. The kinds of changes predicted in phenology or range due to climate change present a challenge for the goal of protecting



Over the last three decades the range of at least one species of bumble bee in the Colorado Rockies has moved fifteen hundred feet higher in elevation. *Bombus flavifrons* on lupine (*Lupinus argenteus*), photographed in Colorado by David Inouye.

habitat for pollinator species. If we protect habitat where pollinators occur today, what will happen in the future as their ranges change? The growing realization of the economic and ecological significance of pollinators may help to spur the research that is needed to increase our understanding of the changes they are facing and provide better strategies for protecting these vital creatures.

David Inouye is a professor of biology at the University of Maryland, College Park. He has worked at the Rocky Mountain Biological Laboratory since 1971, studying hummingbirds, pollination biology, ant-plant mutualisms, bumble bees, and the phenology and demography of wildflowers. Inouye was a member of the National Research Council committee on the status of pollinators in North America.

Conserving Our Most Important Native Pollinators

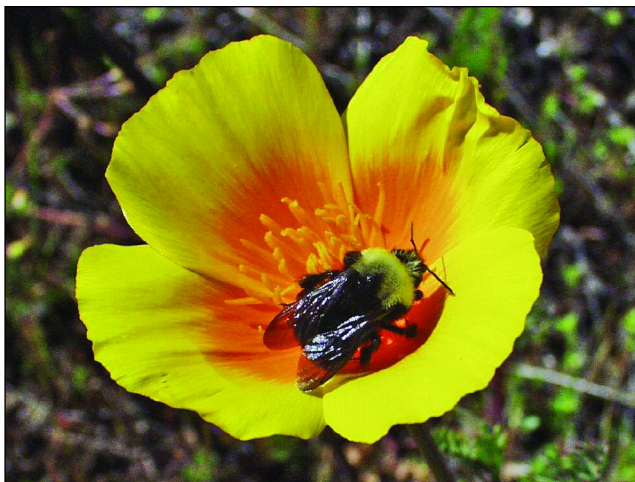
Seven years ago, bee taxonomists began to notice a decline in the abundance and distribution of several very common bumble bee species across the United States. Three bee species, *Bombus occidentalis* (the western bumble bee), *B. affinis* (the rusty-patched bumble bee), and *B. terricola* (the brown-tipped bumble bee), were once very common and important crop pollinators across North America, but are now only rarely found. A fourth species, *B. franklini* (Franklin's bumble bee) may already be extinct.

The decline of these species is correlated with a crash in the laboratory populations of commercially raised bumble bees that were distributed across North America for greenhouse pollina-

tion. This coincidental timing suggests that an exotic disease is the cause for the widespread loss, although this hypothesis is still in need of validation.

The Xerces Society is collaborating with a bumble bee expert, Dr. Robbin Thorp, to learn the former and current ranges of these species. We are soliciting information from the scientific literature, museum collections, and experts across the country to document the bees' former range and abundance; and we are conducting background research on each species' biology, ecology, and role in crop pollination. This information will help determine the best way to protect the populations that remain.

We are also working to raise public



An introduced disease carried by commercially raised bumble bees may be the cause of decline in native species, including Franklin's bumble bee (*Bombus franklini*). Photographed in Oregon by Dr. Peter C. Schroeder.

awareness about these species, their role in pollination of crops and natural areas, and the threats they face. We are creating a series of "Wanted" posters to send to bee researchers and entomology and ecology departments across the country, as well as to annual meetings of groups such as the Entomological Society of America and the Society for Conservation Biology. The purpose of the posters is to educate the public and scientific community about the decline

of these bees and to solicit information about their current distribution.

In addition to protecting the populations of these declining bumble bees, we hope to prevent the unregulated transport of bumble bees (and their diseases) in order to prevent future declines in other bumble bee species.

Funding for this project comes from the CS Fund. To find out more about this effort please visit www.xerces.org/bumblebees.

Partnership with the Natural Resources Conservation Service

For five years we have been building a program focused on pollinator conservation in agricultural landscapes. On July 20, 2007, the Xerces Society signed a memorandum of understanding with the Natural Resources Conservation Service that is helping us to expand our outreach to a broader segment of the agricultural community.

We are working with NRCS offices across the country to provide pollinator conservation and management training and to help NRCS staff incorporate pollinator conservation into existing farm bill programs. This effort has been funded by Xerces members together with the Turner Foundation and other private foundations.

Xerces Works to Understand and Protect Wetlands

In the past century, millions of acres of wetlands in North America have been lost due to agriculture or urbanization. Many of the remaining wetlands suffer from a variety of human impacts, including pollution, changes in water flow, and invasive species.

Wetlands are important elements of watersheds, providing such valuable ecosystem services as water filtration, flood control, erosion control, and critical habitat for animals and plants. Quality wetland habitat is essential to native and endangered species; about half of all federally listed endangered animals rely on wetlands for survival, including over 50 percent of America's

protected migratory bird species.

In the Pacific Northwest, many wetlands are severely compromised but few have been studied thoroughly and little information is available on their biological integrity (their ability to support life). While there are a variety of techniques available to assess the biological condition of rivers and streams, evaluation of the biological attributes of wetlands and their responses to human disturbances has lagged behind. An increasing number of watershed councils in the Northwest are taking on wetland restoration projects, but lack the tools to assess wetland quality and evaluate restoration success.



Sarina Jepsen, Xerces Society senior conservation associate, uses a dip net to collect aquatic invertebrates as part of our effort to develop a biological assessment tool for wetlands. Photograph by Logan Lauvray.

The Xerces Society is working to develop an invertebrate-based biological assessment tool that can be used to assess wetland quality. With funding from the Environmental Protection Agency and the Mountaineers Foundation, we completed a pilot project to identify the invertebrates in one class of wetland and have begun developing this assessment tool for the Pacific Northwest. Next year we hope to expand the project to include additional classes of wetland.

The information and recommenda-

tions drawn from background research and our pilot study have been incorporated into a CD-ROM guide to wetland invertebrate identification in the Pacific Northwest. The guide has family-level keys for aquatic invertebrates encountered in Northwest wetlands, and general information on invertebrate monitoring in still water habitats. To purchase the CD-ROM *Aquatic Invertebrates in Pacific Northwest Freshwater Wetlands: An Identification Guide and Educational Resource*, please go to www.xerces.org.

Support Butterfly Conservation: Pledge the Butterfly-A-Thon

Throughout 2008, noted lepidopterist and writer Robert Michael Pyle will be undertaking a historic journey to find, experience, and identify as many species of butterflies as possible in the United States and Canada. The literary fruits of this project will be published by Houghton Mifflin as a book entitled

Swallowtail Seasons: The First Butterfly Big Year. The project is also a fundraiser, and you can participate in this effort by making a pledge for every butterfly species that Bob encounters, as part of a "Butterfly-A-Thon." All proceeds from the Butterfly-A-Thon will go towards the Xerces Society's work to preserve

and protect rare and endangered butterfly species.

During his travels, Bob will be seeking to find as many as he can of the nearly eight hundred butterfly species recorded in North America north of Mexico, although the numbers will be secondary to his actual encounters with the butterfly fauna. To update participants on his progress, he will be posting regular updates from the road on a Butterfly-A-Thon blog.

Bob Pyle founded the Xerces Society in 1971. He has published fifteen books, including such butterfly classics as the *Audubon Society Field Guide to North American Butterflies*, the *Handbook for Butterfly Watchers*, and *The Butterflies of Cascadia*, as well as award-winning literary works, including *Wintergreen* and *Sky Time in Gray's River*.

To make a pledge or to find out more about the Butterfly-A-Thon, please visit www.xerces.org.

New Staff Members at the Xerces Society

We are delighted to have two new staff members at Xerces.

Celeste Mazzacano joins us as a conservation associate. Celeste holds a Ph.D. in entomology from the University of Minnesota. She has more than twelve years of experience in research, education, and conservation, and has worked extensively with aquatic invertebrates. At Xerces she is currently de-

veloping assessment tools for wetlands of the Pacific Northwest.

Lisa Schonberg is our new conservation assistant. She recently completed her M.S. in entomology at Evergreen State College, researching ants in the cloud forests and lowland forests of Costa Rica. Lisa will be working on a variety of pollinator conservation and endangered species projects.

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For information about membership and our conservation programs for native pollinators, endangered species, and aquatic invertebrates, contact us:

THE XERCES SOCIETY FOR INVERTEBRATE CONSERVATION

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Individual coral polyps are usually tiny, but in colonies can form massive stony formations, such as this brain coral (*Oulophyllia crispa*). Coral reefs are among the first ecosystems to display signs of significant damage due to global warming. Photographed in Tanzania's Songo Songo archipelago by David Obura.

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Our cover photograph shows an Apollo butterfly (*Parnassius apollo*). Butterflies are one of the best studied insects with respect to the impacts of climate change; the range of this species has shifted due to global warming. Photographed in Italy by Angie Sharp.