Conserving the Jewels of the Night

Guidelines for Protecting Fireflies in the United States and Canada

Candace Fallon, Sarah Hoyle, Sara Lewis, Avalon Owens, Eric Lee-Mäder, Scott Hoffman Black, and Sarina Jepsen

XERCES SOCIETY
for Invertebrate Conservation

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Photographs and Artwork
Cover: A female big dipper firefly (*Photinus pyralis*) signals to a potential mate. (Photograph: Radim Schreiber, fireflyexperience.org.)

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Fireflies are some of our most beloved insects. Watching fireflies, such as these mystical lantern fireflies (*Photuris mysticalampas*) in an Atlantic white cedar forest in Delaware, is a treasured summer evening pastime. (Photograph: Radim Schreiber, fireflyexperience.org.)

Executive Summary

Fireflies are some of our most celebrated insects. They have immense cultural, biological, and economic importance and are important components of natural ecosystems. Their public appeal also makes them ideal flagship species for conservation.

Fireflies are not flies but actually beetles in the family Lampyridae. They are found all over the world, on every continent except Antarctica, living in temperate and tropical areas. More than two thousand species have been described, with nearly 170 in the United States and Canada. More species are being discovered and described each year. At the same time, firefly populations appear to be in decline. Recent news articles carry headlines such as "Firefly Populations Are Blinking Out" and "Are Fewer Fireflies Lighting Up the Skies?" While long-term monitoring studies of fireflies are sparse, a growing number of anecdotal reports, backed by expert opinion, suggest that fireflies are indeed declining. This concern gains greater significance in light of numerous diversity, abundance, and biomass studies that have emerged in recent years documenting severe population declines in better-studied insect groups. We need to study firefly populations more closely to fully understand their plight and ensure conservation efforts are effective.

The causes of these reported declines are not well known, but may well include some combination of habitat degradation and loss, light pollution, pesticide use, climate change, and introduced species. Tourism increases in places where fireflies flash in synchrony may also be contributing to local declines. Regardless of the specific reasons, researchers agree that protecting, restoring, and enhancing firefly habitat is one of the best ways to conserve their populations. In addition, collecting baseline data on firefly populations and distributions will contribute to a better understanding of their conservation status.

In this document, we outline the importance of fireflies and describe their life histories and threats to their populations. We then provide steps you can take to create and manage habitat, influence policies that benefit fireflies and their habitats, and raise awareness of this special group of beetles. We also provide a summary of the firefly genera found in the United States and Canada (Appendix A) and a list of resources for learning more (Appendix B). Throughout, you will find short case studies and examples of people doing more to help fireflies, which we hope will inspire you to take action in your own way.

The big dipper firefly (*Photinus pyralis*) is one of our most commonly encountered species, but it is one of nearly 170 described species in the United States and Canada. Researchers and firefly enthusiasts alike are concerned that populations of some firefly species may be declining. (Photograph: Ivan Kuzmin.)

Glow-worm fireflies are more commonly found in the West, where glowing females can sometimes be seen in leaf litter.
(Photograph: Radim Schreiber, fireflyexperience.org.)

1

Introduction

What Is a Firefly?

Fireflies, which are also called lightningbugs and glow-worms, are actually beetles (order Coleoptera) in the family Lampyridae. The common name *firefly* includes not only our familiar flashing species, but also the more cryptic glow-worms and our daytime dark fireflies, whose adults—as their name suggests—are active during the day and rely on chemical pheromones rather than bioluminescence to communicate (Table 1; Appendix A). Glow-worms, like flashing fireflies, are active during dusk or nighttime and use bioluminescence (by glowing, not flashing) to communicate. While males look like typical fireflies, glow-worm females resemble larvae; they cannot fly because their wings are short or even absent.

Fireflies are in every continent except Antarctica, every US state except Hawaii, and all of the lower Canadian provinces. It is often thought that fireflies occur only in the central and eastern United States and Canada. Although these areas tend to have more species, fireflies are widespread across both countries (Figure 1). The more conspicuous flashing species occur primarily in the East. In the West, glow-worms (species in which females glow to attract mostly nonluminescent males) and day-active dark fireflies (which also have glowing larvae) make up the majority of species. Flashing species can be found in some localized areas of the West—reports have surfaced from Colorado, Wyoming, Montana, Arizona, Nevada, Utah, and California, among other states (Faust 2017).

Table 1: Firefly Genera of the United States and Canada

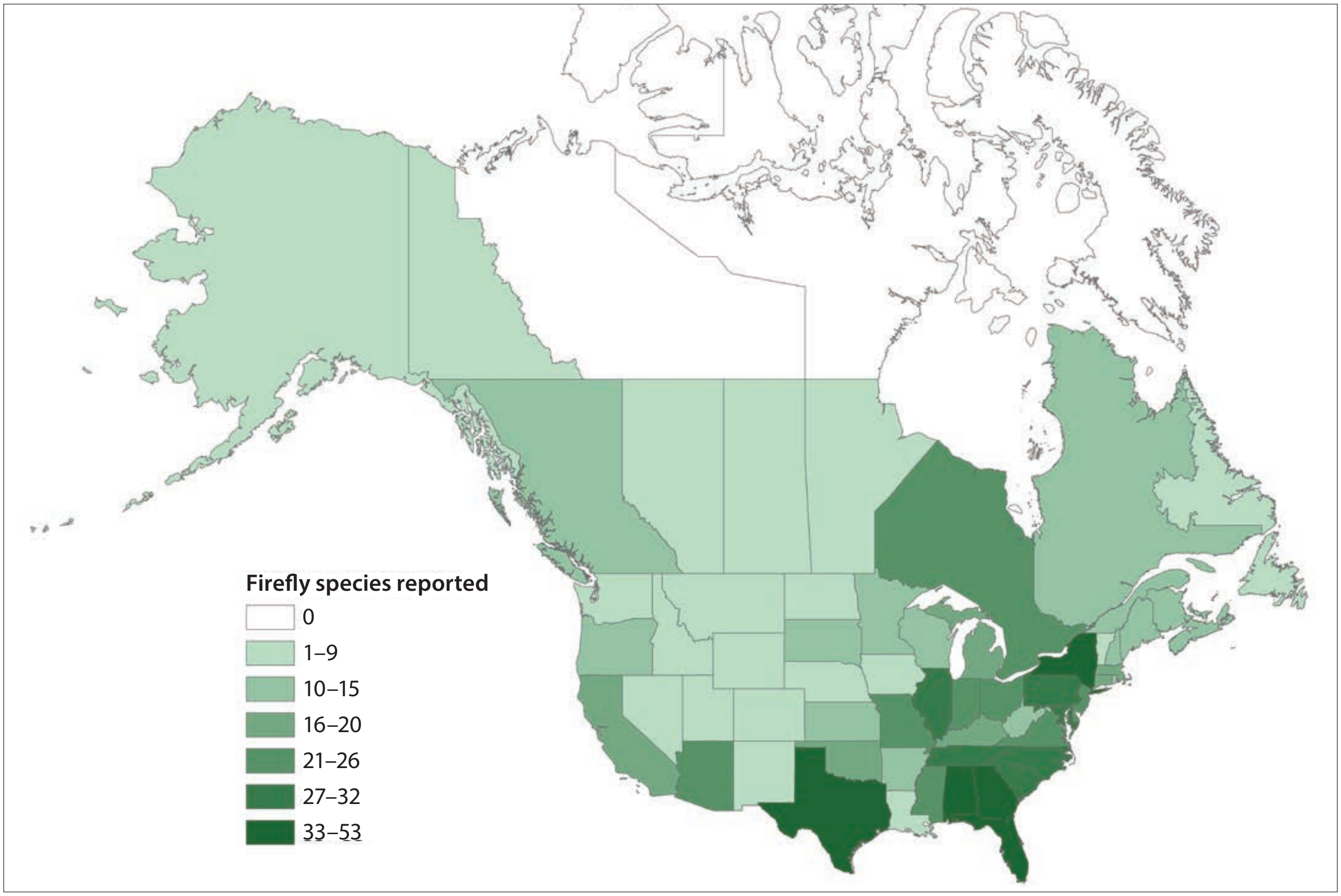
Subspecies given in parentheses.

Flashing Fireflies		Glow-Worms		Daytime Dark Fireflies	
Genus	**No. Species**	**Genus**	**No. Species**	**Genus**	**No. Species**
Aspisoma	1	*Microphotus*	7	*Brachylampis*	2
Bicellonycha	1 (2 ssp.)	*Nelsonphotus*	1	*Ellychnia*	16
Micronaspis	1	*Phausis*	10	*Lucidota*	3
Photinus	34*	*Pleotomodes*	2	*Paraphausis*	1
Photuris	61	*Pleotomus*	3	*Pollaclasis*	1
Pyractomena	16	*Prolutacea*	1	*Pterotus***	2
				Pyropyga	4
				Tenaspis	1
114 species (2 subspecies)		**24 species**		**30 species**	

* Two *Photinus* species do not flash, but are thought to use pheromones.
** One species of *Pterotus*, *P. curticornis*, appears to be active at night.

Figure 1: Approximate Number of Firefly Species Reported by State, Province, or Territory

Source: Xerces Society 2019, unpublished data. Note: this map is a work in progress and may change as more records are added to our database.



Importance of Fireflies

Fireflies are some of our most cherished and celebrated insects, dazzling us with their beautiful light displays and playing important roles in human medicine, technology, and culture. Ecologically, they are significant predators in local food webs and serve as prey to other animals. In the wake of mounting anecdotal evidence of firefly declines, the global research community is taking note. In August 2010, firefly researchers, enthusiasts, and conservationists from 13 countries gathered in Selangor, Malaysia, for the Second International Firefly Symposium. Representing a wide range of fields, from taxonomy and behavior to genetics and ecology, these participants came together to discuss a unifying theme: firefly conservation. An important outcome of this meeting was the development of the Selangor Declaration, a document urging worldwide governments to protect and restore firefly habitat, educate and promote the involvement of local communities, and support basic and applied research. The declaration succinctly outlines the importance of fireflies, which we explain in detail in this section.

Ecological Role

Fireflies contribute to food-web stability, playing important roles as both predators and prey. Firefly larvae are voracious carnivores, feeding on a variety of soft-bodied invertebrates, including snails, slugs, and earthworms. Because of their large appetites and preference for snails and slugs, fireflies can be highly beneficial in gardens and agricultural settings. Larvae of some species can also be omnivorous, and have even been observed eating berries and other organic matter on the ground (Lewis 2016a). Adults rarely feed, with one notable exception: females of several *Photuris* species (widespread throughout North America) prey upon the males other firefly species, including those in their own genus and in *Photinus* and *Pyractomena*. Most fireflies are toxic due to defensive compounds known as lucibufagins (LBGs), but these *Photuris* females lack the toxin. To make up for this, and in order to pass on a means of defense to their young, these females feast on fireflies that do contain LBGs.

Lucibufagins are to fireflies what milkweed cardenolides are to monarchs—highly toxic substances that protect them from many predators, including birds, toads, and lizards. Yet despite the bad taste afforded by these chemicals, and the warning glows and cautionary colors that many species advertise, fireflies contribute to the diets of a number of other animals. Spiders are the best-documented invertebrate predators of fireflies (Lloyd 1973). For example, De Cock et al. (2014) observed numerous instances of spider predation on the blue ghost firefly (*Phausis reticulata*) by orb weavers, sheet-web weavers, and a single black widow in the eastern United States. Long et al. (2012) noted predation by jumping spiders. In an interesting twist, kleptoparasitism has also been documented—hungry *Photuris* will snatch firefly prey from spider webs (Faust et al. 2012a; Alcock 2018). Numerous other invertebrates have been observed feeding on fireflies, including harvestmen, cobweb spiders, assassin bugs, and hangingflies (Lewis et al. 2012). Vertebrate predators appear to be more affected by the toxins found in fireflies, and predation by these animals occurs less frequently.

Aesthetic Inspiration

Fireflies—particularly flashing and glowing fireflies—have captured the human imagination for centuries. These iconic insects have frequently been the focus of art, literature, and cultural traditions. The spectacular courtship displays of some synchronous species are particularly inspiring. Ecotourism of synchronous firefly displays has long been established in parts of Asia, but is relatively new to the United States. The best-known firefly event in the United States is probably the annual light show hosted by the Great Smoky Mountains National Park in North Carolina and Tennessee. The show has become so popular that the park has created an annual lottery system to view their famous synchronous fireflies (*Photinus carolinus*). Other fireflies are starting to get attention, too. The otherworldly *Phausis reticulata*, or blue ghost fireflies, can be seen in North Carolina's DuPont State Forest or in South Carolina at the Firefly Forest, a property managed

Light trails of the blue ghost firefly (*Phausis reticulata*) are seen in the Blue Ridge Mountains of North Carolina. (Photograph: Radim Schreiber, fireflyexperience.org.)

Bioluminescent fireflies have light organs located on the tips of their abdomens, as can be seen in this big dipper firefly (*Photinus pyralis*). (Photograph: Terry Priest, Flickr CC BY-SA 2.0.)

by Don Lewis. The Pennsylvania Firefly Festival celebrates synchronous fireflies and others each year in the Allegheny National Forest. Visitors arrive from all over the country to take in these shows, bringing money to both the parks and nearby businesses for several weeks each summer. Flashing fireflies are also becoming an attraction in some state parks in the Midwest and in a few areas of western Colorado, drawing people in to see their nighttime displays.

Scientific Research

Fireflies have played important roles in biomedical research. Fireflies produce light through a chemical reaction involving oxygen, a light-emitting biological compound called luciferin, and an activating enzyme called luciferase. Decades ago, luciferase caught the attention of researchers who have since harnessed its glow to observe interactions within cells, leading to a wide array of medical advances. Luciferase has been used to visualize HIV transmission, improve the detection of blood clots, and better understand diseases like Parkinson's. In addition, it is widely used in kits that test for bacteria contamination in milk, meats, and other products; any microbes present in these foods will light up. Biomedical researchers now use luciferase to tag tumor cells in live animals, providing a powerful way to identify new anti-cancer drugs. In the late 20th century, millions of fireflies were collected and sent to research companies to isolate this enzyme (Lewis 2016b). Fortunately, in the mid-1980s a synthetic version was created, eliminating the need to harvest wild fireflies for their luciferase.

In recent years, community science efforts have emerged to document the distribution and habitat associations of our resident firefly fauna. These projects not only contribute valuable data to researchers, but they also provide participants a form of recreation and a critical connection to nature.

Flagship Species

Fireflies make ideal flagship species, given the near-universal human enchantment with them. Flagship species are species with broad appeal that can help raise conservation awareness by gaining public and political sympathy. Fireflies do not sting or bite, they are not crop or garden pests (in fact, they can help control crop and garden pests), and they are celebrated around the world for their beauty. By raising awareness of fireflies and their needs, we can also help a suite of other species of flora and fauna that depend on the same types of habitats in which fireflies are found, including tidal marshes, bogs, river canyons, and other wetland areas. Because of their sensitivity to light pollution and water degradation, fireflies also make ideal bioindicators (used to assess ecosystem health and function on a large scale).

2

Life History and Mating

Life Cycle

Like all beetles, fireflies undergo complete metamorphosis with four distinct stages: egg, larva, pupa, and adult. Most of their life cycle is spent in the larval stage: they spend up to two years as larvae, but adults typically live for just two to four weeks (Faust et al. 2012b). The complete life cycle can take anywhere from a couple of months in the southern United States to two or three years in the northern United States and Canada (Lloyd 2006). After mating, females lay their eggs in moist soil, duff, leaf litter, or rotting wood. Eggs, which may glow dimly, are deposited in batches or singly during periods ranging from several days to weeks (Lloyd 2018). Two to three weeks later, these eggs hatch into grub-like beetle larvae that live in leaf litter, underground, or in rotting wood. All firefly larvae are bioluminescent (Lloyd 2018), an adaptation thought to warn potential predators that they are distasteful (Lewis 2016a). In southern latitudes, larvae can stay active year-round, while farther north they become inactive underground during winter months. Although firefly larvae are rarely seen, the intermittent glows of foraging *Photuris* or other larvae can sometimes be seen on dark nights in fall and spring.

Firefly larvae are voracious predators of soft-bodied invertebrates, including snails, slugs, and earthworms. Larvae typically hunt for their prey in moist soil or marshy areas near springs, ponds, and creeks (Buschman 2016). Some species are dietary generalists, whereas others specialize in eating snails, earthworms, or potentially even ant larvae (eaten by *Micronaspis floridana*, *Photinus* spp., *Pleotomodes* spp., respectively) (Lloyd 2018). Firefly larvae use their mandibles to inject prey with paralyzing neurotoxins, and then

Firefly larvae are voracious predators of soft-bodied invertebrates such as snails, slugs, and earthworms. (Photographs: top, Katja Schulz, Flickr CC BY 2.0; bottom, Heinz Albers, Wikimedia CC BY-SA 3.0.)

secrete digestive enzymes that liquefy the prey before ingestion (Lewis 2016a). Although firefly larvae are mainly carnivorous, Faust and Faust (2014) found that *Photuris* larvae in captivity feed on milkweed rhizomes.

When fully grown, most firefly larvae pupate underground or in rotting logs. Some *Pyractomena* larvae, however, climb trees and attach themselves to bark before they undergo pupation. Depending on temperature and species, pupation can last one to three weeks (Lloyd 2018), with firefly adults typically emerging in late spring or early summer.

A surprising exception to this typical life cycle is seen in winter fireflies (*Ellychnia corrusca*), which overwinter as adults rather than as larvae. In this species complex, adults congregate in the fall and seek refuge in the deeply furrowed bark of large trees, sometimes using the same overwintering trees year after year (Faust 2012). These long-lived adults can survive for up to 10 months while overwintering on trees (Rooney and Lewis 2000).

Mild winters can lead to early emergence and larger numbers of fireflies (Evans et al. 2019), since these conditions may lead to better survival of overwintering larvae. For similar reasons, warm, wet springs can also lead to earlier or larger displays, and these conditions may also favor larval fireflies' favorite prey. Different species require different amounts of time for their development (Weston and Faust 2012). Adults of certain species emerge in early spring, while others emerge later in summer. The exact emergence dates can vary considerably depending on location and environmental variables such as temperature and rainfall. Warmer southern regions may host two cohorts for some species, with one peak of adult emergence in spring and another in fall. Farther north, one generation is more typical. In some species, their mating season may last only a week or two, while in others the mating season may last for several months.

Bioluminescence

Every member in the family Lampyridae creates light using the same biochemical reaction, which takes place inside both larval and adult light organs, or lanterns. The firefly luciferase enzyme allows its substrate, known as luciferin, to interact with oxygen and the chemical ATP to produce a photon of light. First originating in larval fireflies, this light-producing talent is thought to have evolved as a warning signal that alerted potential predators to distasteful or toxic compounds. Over evolutionary time, certain fireflies later co-opted this larval bioluminescence into an adult courtship signal.

Different firefly species can emit different colors (wavelengths) of light varying from green to yellow to red, apparently due to small chemical differences in the microenvironment of the luciferase-luciferin pair. Firefly species active around twilight tend to emit yellower flashes, perhaps because these are easier to detect against the background of green light reflected off foliage, while those active in full darkness tend to emit greener flashes (Lall et al. 1982; Lall and Lloyd 1989; Endler 1993).

Firefly species that flash in full darkness tend to emit greener light than those that flash at twilight. (Photograph: Benjamin Lehman, Flickr CC BY-NC-ND 2.0.)

Fireflies can be split into three main groups: daytime dark fireflies like the black firefly (*Lucidota atra*; top), glow-worms such as the California pink glow-worm (*Microphotus angustus*; bottom left), and flashing fireflies like *Photuris* (bottom right). (Photographs: top, Katja Schulz, Flickr CC BY 2.0; bottom left, Ken-ichi Ueda, Flickr CC BY-NC 2.0; bottom right, Warren Lynn, Flickr CC BY-ND 2.0.)

Adult Courtship

Fireflies are best known for their bioluminescent courtship displays, yet not all adults are capable of producing light (Lloyd 2008). Fireflies can be categorized into three main groups:

- Daytime dark fireflies: Adults are active during the daytime and do not produce light. Instead, females attract males by emitting chemical signals known as pheromones. The black firefly (*Lucidota atra*) is one common US daytime dark firefly.
- Glow-worms: These females produce long-lasting glows and cannot fly because they lack functional wings. The blue ghost firefly (*Phausis reticulata*) is a glow-worm found in the southeastern United States, while the California pink glow-worm (*Microphotus angustus*) is found on the West Coast.
- Flashing fireflies (a.k.a. lightningbugs): Adults court by exchanging quick, bright flashes. In the United States and Canada, this group includes all *Photuris* and *Pyractomena* species and most *Photinus* species.

Most of the flashing species found in the United States and Canada engage in flash dialogs during courtship. To attract the attention of females, flying males emit a particular flash pattern while patrolling an area. Females generally do not fly, but instead perch on low vegetation or on the ground. If a female is interested, she will respond to the male by flashing back. This flash dialog can continue for more than an hour until the male finally locates the female and they mate. Male flash patterns vary by species and may consist of single, double, or multiple pulses repeated at regular intervals. In *Photinus* fireflies, these flash patterns can be used to distinguish species. In *Photuris* fireflies, flash patterns are highly variable and individuals often emit different flash patterns depending on the time of night.

The mating displays produced by certain synchronously flashing fireflies are a spectacular natural phenomenon. For unknown reasons, in only a few species do males have this special ability to flash in unison. In the United States and Canada, synchrony occurs in *Photinus carolinus*, which is found in Tennessee and North Carolina in the Great Smoky Mountains as well as in the Allegheny National Forest in Pennsylvania. Another synchronous species is *Photuris frontalis*, found in Congaree National Park in South Carolina. Perhaps synchrony helps these females detect the specific flash pattern given by their own males; in a dense population of constantly moving males, this pattern may be difficult for females to discern unless males synchronize their flashes (Moiseff and Copeland 2010).

Top: Mating fireflies can remain coupled for several hours. Bottom: While bioluminescence is important for flashing species to find their mates, it can also be a trick. Females of some *Photuris* species will mimic the flash of other fireflies to lure them in for dinner. (Photographs: top, Brenda Dobbs, Flickr CC BY-NC 2.0; bottom, Joyce Gross.)

Fireflies also partition their courtship activity into different times of night. Some fireflies begin courting at dusk, and their courtship may last for just 20 minutes. Other species become active only when it is fully dark and may continue courtship for a few hours. Firefly flashing also depends on temperature, with faster flash rates and more activity occurring on warmer nights.

Mating and Reproduction

Because most fireflies do not eat once they become adults, their reproductive activities must be fueled by whatever resources they have stored from larval feeding. Fireflies have long mating durations, with pairs remaining coupled for one to several hours. During this time, males transfer to their mate an elaborate sperm-containing package known as a nuptial gift (Lewis and Cratsley 2008). These gifts contain proteins that increase the number of eggs the female will produce. Although both sexes can mate multiple times, gift size steadily declines across sequential matings. Males of glow-worm fireflies do not provide such gifts and, typically, these females will mate only once, lay eggs, and then die. Females of the glow-worm *Phausis reticulata* guard their eggs (De Cock et al. 2014), which may protect against egg predators.

Case Study

Bethany Beach Firefly Threatened by Development

Recent development in the Breakwater Beach residential area in Delaware has destroyed interdunal swale habitat of the largest known population of the Bethany Beach firefly (*Photuris bethaniensis*). (Photograph: Emily May.)

Despite decades of anecdotal reports of firefly declines in the United States, the conservation needs and population trends for the majority of our nearly 170 species are largely unknown. One stark exception to this is the Bethany Beach firefly (*Photuris bethaniensis*), a small firefly characterized by its double green flash and narrow distribution along a 20-mile stretch of Delaware's Atlantic coast.

In 2019, the Xerces Society and the Center for Biological Diversity submitted an emergency petition to list this firefly as endangered under the Endangered Species Act (ESA) (Cornelisse et al. 2019). Although already listed as an endangered species at the state level, this firefly has received little conservation attention. It is known from just seven sites and is closely associated with an uncommon habitat type known as interdunal swales. These swales, formed in small depressions behind coastal sand dunes, are fed by freshwater and support unique plant communities.

The Bethany Beach firefly's largest-known population is slated for residential development, and construction has already affected the wetland they call home. The six remaining populations may be too small to support the persistence of this species over the long term, although they are better protected because they are located on Delaware State Parks lands. An emergency ESA listing would protect this firefly from imminent extinction by addressing current threats, including habitat loss and fragmentation. As a result, the Bethany Beach firefly could become an ambassador for freshwater wetland health in the state and an important conservation icon as Delaware's only known endemic species.

Adult Feeding

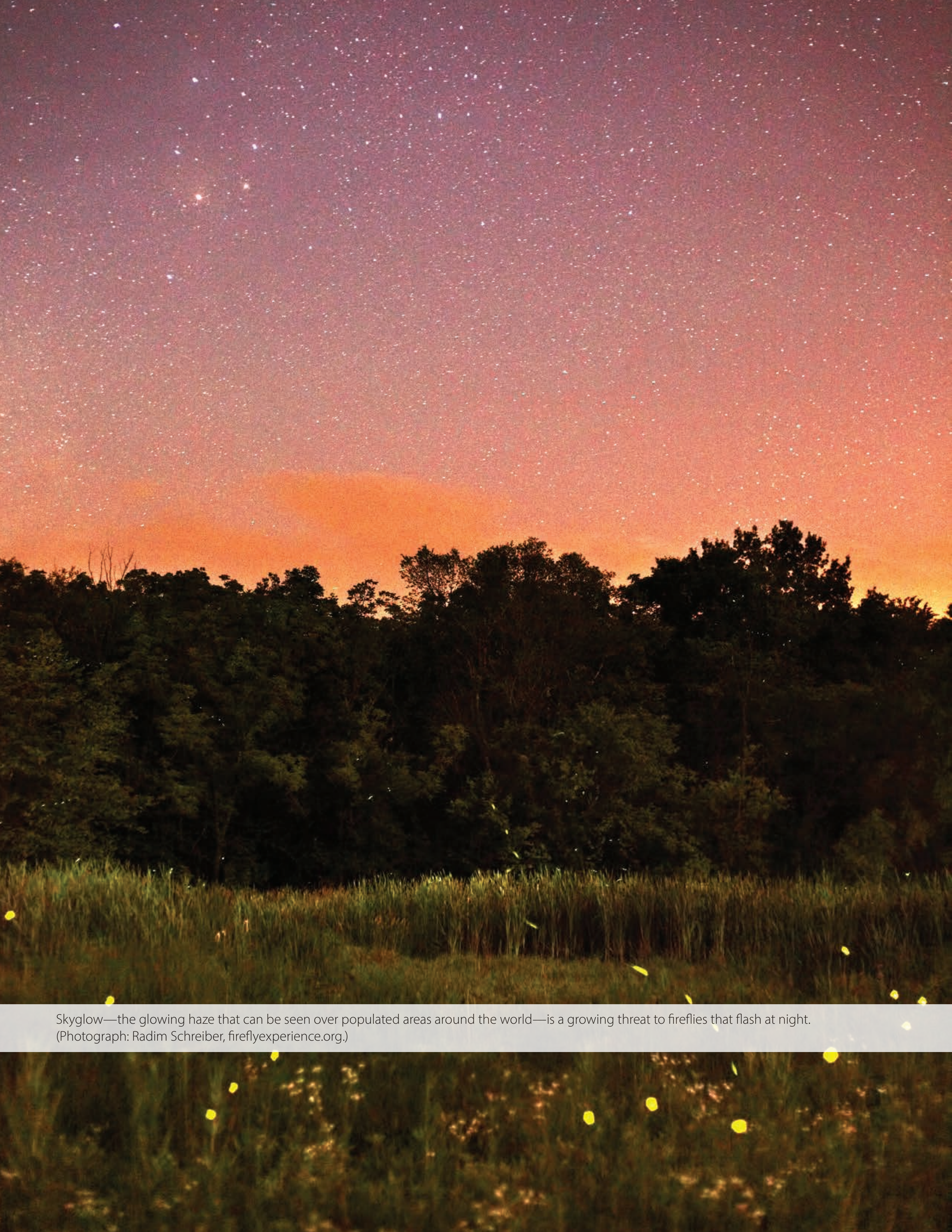
A striking exception to the general rule that most adult fireflies do not feed comes from certain fireflies belonging to the genus *Photuris*. These females are able to mimic their prey's courtship flashes to lure in males of other firefly species. These predatory *Photuris* females also obtain prey by attacking flying males and stealing fireflies from spider webs. By consuming other fireflies, such predatory fireflies obtain and sequester defensive chemicals that they then use to protect themselves and their eggs. Limited observations have also been made of adult feeding by other firefly species on plant tissues and nectaries, including *Ellychnia corrusca* adults feeding on maple sap and aster, goldenrod, and maple flowers (Rooney and Lewis 2000). Faust and Faust (2014) found adults of five species from four genera feeding on and associated with common milkweed (*Asclepias syriaca*).

Habitat Associations

Fireflies are associated with a wide range of habitats, yet they all seem to have one element in common—moisture. Fireflies have been documented in interdunal freshwater depressions (*Photuris bethaniensis*) (Heckscher and Bartlett 2004), grasslands (*Pyractomena angulata*) (Lloyd 1996), desert canyons (*Photinus knulli*) (Cicero 1983), and more. Some species are highly specialized, whereas others are generalists, occupying a range of damp meadows, forests, and marshes. An extreme example of habitat specialization can be seen in the two species of *Pleotomodes*, found in Florida and the southern United States. Both the larvae and adult females of this genus are associated with ant nests, although researchers are not certain why.

Depending on their life stage, fireflies require different microhabitats. Eggs and larvae may be found in moss, on the soil surface, under duff and leaf litter, or in rotting wood. Pupae can be found underground, in leaf litter, in small earthen chambers, or attached to herbaceous vegetation or tree trunks. Wingless glow-worm females do not stray far from their natal sites and may seek cover under leaves or twigs or in abandoned rodent burrows. Winged males and females may fly farther afield and can be found throughout canopy layers or on emergent vegetation. In the eastern United States and Canada, fireflies may use ephemeral habitats such as irrigated lawns, agricultural fields, or damp meadows. In the West, fireflies are restricted to areas with permanent water sources, including streams, rivers, lakes, and springs (Buschman 2019, pers. comm.).

Fireflies are found in a wide variety of habitats, from mixed-age deciduous forests on the East Coast to desert mountain canyons in the West. The most important feature for most species is the availability of water. (Photographs: top left, Nicholas A. Tonelli, Flickr CC BY 2.0; bottom left, Laura Richardson, Flickr CC BY 2.0; bottom center, Emily May; bottom right, Arizona Traveler, Flickr CC BY-NC-ND 2.0.)



Skyglow—the glowing haze that can be seen over populated areas around the world—is a growing threat to fireflies that flash at night. (Photograph: Radim Schreiber, fireflyexperience.org.)

3

Threats to Fireflies in the United States and Canada

Anecdotal reports from around the world tell of firefly declines. While the extent of declines and their causes are not well understood, we do have a basic understanding of major threats to fireflies, including habitat degradation and loss, light pollution, pesticide use, poor water quality, climate change, invasive species, and overcollection. Fireflies may be most vulnerable during their larval stage, which can last up to two years. Adults, on the other hand, are generally active for only a few weeks each year. Species with specific habitat requirements or narrow or patchy distributions are often more at risk. Certain life-history traits can also increase vulnerability. For example, species requiring true dark for their mating displays will be more affected by light pollution than dusk-active species adapted to higher light levels (Faust 2017, pers. comm.). Species with flightless females may be more vulnerable to local extinctions since these females cannot disperse very far. Lowering water tables—an increasingly common issue across the West and other parts of the country due to groundwater withdrawals and drier climates—can reduce the moist habitat fireflies need. Threats to soft-bodied invertebrates such as earthworms, snails, and slugs may have cascading effects on firefly populations, as these organisms make up the bulk of larval firefly diets.

Habitat Degradation and Loss

Habitat degradation, loss, and fragmentation are considered the largest threats to most declining insect species worldwide and may well be the largest threats to fireflies in the United States and Canada. Commercial and residential development, water pollution, and groundwater pumping are some of the key drivers of this loss and degradation. In general, most firefly species depend on moist habitats, including wetlands, streams, and damp fields. Modification of aquatic habitats, such as dams and channelized irrigation ditches, can negatively affect firefly populations. Drought, disruption of natural water flows, and diminishing water tables may be issues for species in arid areas of the West. In more urbanized areas, loss of leaf-litter habitat required during larval life stages is also a concern. Habitat loss can be especially detrimental for species with flightless adult females, as these females cannot disperse far beyond their natal sites. Flightless females and larvae are also at higher risk of physical crushing. Egg laying, larval and pupal development, and mating all tend to happen at ground level, so any activities that disrupt this area (including earth removal and trampling) can negatively affect firefly populations. For example, trampling by cattle is an issue in ephemeral habitats in the West (Buschman 2019, pers. comm.)—not only do cattle degrade freshwater spring and riparian habitats, their hooves can directly result in mortality. Throughout North America, increasing urban and suburban development threatens already fragmented firefly habitats. In the East, multiple firefly populations have been lost due to new housing developments, road construction, and retail development (Branham 2019, pers. comm.; Faust 2017, pers. comm.), including one of the best-known populations of the rare *Photuris bethaniensis*, a Delaware endemic known only from freshwater interdunal swales along the Atlantic coast (Heckscher 2019, pers. comm.).

Both the brightness and the number of artificial lights at night (ALAN) are increasing to the point that few places are now truly dark. (Image: NASA Earth Observatory image by Robert Simmon, using Suomi NPP VIIRS data provided courtesy of Chris Elvidge, NOAA National Geophysical Data Center.)

Changes in water management and availability may be an important factor in firefly declines in the West and other areas of the United States. Buschman (2016) notes that the water table along the Arkansas River in western Kansas has fallen so dramatically that many of the springs and marshes that used to exist are now dry; at the same time, firefly populations in these areas are now gone.

Light Pollution

Light pollution comes in several forms, including skyglow (the glowing haze over highly populated areas), light trespass (light that reaches beyond its intended or needed area), and glare (light that excessively illuminates areas or objects). It can be caused by street and house lights, vehicle headlights, billboards, and even gas flares from oil fields. All sources of artificial light at night, or ALAN for short, have the potential to drive declines in firefly populations. Unfortunately for fireflies and other affected species, including humans, night sky brightness worldwide is only continuing to increase in both intensity and extent (Kyba et al. 2017). The brightness and number of artificial lights installed in the United States and Canada have increased so dramatically in the last few decades that few areas are now truly dark at night. In fact, more than 80% of people in North America can no longer see the Milky Way on even the clearest nights because it is obscured by skyglow (Falchi et al. 2016).

Lights negatively affect many invertebrates and other animals. ALAN has been implicated as a threat to nocturnal pollination, natural pest control, and seasonal migration patterns, among other processes (Knop et al. 2017; Grubisic et al. 2018; Desouhant et al. 2019). More than 60% of invertebrates are nocturnal (Hölker et al. 2010), which means many of these species are especially likely to be affected by the introduction of ALAN into their habitats. Fireflies are particularly at risk—more than three-quarters of firefly species in the United States and Canada are nocturnal or crepuscular (active at dusk), and these species use light of their own making to communicate. Researchers have speculated that artificial light from street lamps, residences, and other sources may obscure natural firefly bioluminescence, with potentially catastrophic outcomes for species that depend on these signals to find mates or ward off predators (Ineichen and Rüttimann 2012). A growing body of research supports this assertion (Owens and Lewis 2018).

Multiple studies in various regions have found that artificial lights can change firefly occurrence or behavior. In urban areas of Turin, Italy, researchers found significantly lower measurements of illuminance in sites where *Luciola italica* fireflies were observed, compared to places where they were absent (Picchi et al. 2013). Hagen et al. (2015) investigated the effects of floodlights on a species of *Photinus* in Brazil and found that the average number of firefly flashes counted in transects declined sharply when the floodlights were on. In another study in Great Britain, researchers discovered that even very low light levels could interfere with the ability of male glow-worms (*Lampyris noctiluca*) to find glowing females (Bird and Parker 2014). Meanwhile, in controlled field and lab experiments, ALAN has been shown to inhibit the flash activity of several species of fireflies—including *Photinus marginellus, Photuris versicolor, Pteroptyx maipo,* and *Aquatica ficta* (Yiu 2012; Costin and Boulton 2016; Firebaugh and Haynes 2016; Owens et al. 2018)—which could have severe repercussions for the courtship success, and thus population persistence, of these species.

Pesticide Use

Pesticides—including insecticides and herbicides—have been implicated in the declines of many insect species and may be affecting firefly populations. While there is very little research on the direct effects of pesticides on fireflies, their vulnerability can be assessed from research on similar species and firefly prey, as well as observations from firefly researchers. Since most species spend the majority of their lives as larvae consuming earthworms, slugs, and snails, pesticide impacts on these food sources are likely to have negative consequences for fireflies. Herbicides also have the potential to indirectly affect firefly populations by eliminating vegetation needed for shelter, forage, overwintering, and mating.

Pesticides, including insecticides and herbicides, can harm or kill fireflies and affect their habitat or prey. (Photograph: US National Park Service.)

Fireflies can be exposed to pesticides in a variety of ways—via direct applications to their habitat, runoff from agricultural or ornamental applications, or consumption of contaminated prey. Their reliance on moist habitats means they are vulnerable to pesticides moving through water. Flashing adult fireflies tend to get most of our attention, but it is important to consider how pesticide use can affect each life stage (from egg to larva to pupa to adult) throughout the year. Larvae and flightless adult females are likely the most vulnerable to pesticides because they are relatively immobile and unable to disperse away from treated sites.

Among pesticides, insecticides are the type most likely to directly harm fireflies since they are designed to kill insects, including beetles. Laboratory experiments conducted on the Asian firefly species *Aquatica lateralis* showed that several common insecticides (including the neonicotinoid thiamethoxam; the organophosphates acephate, fenthion, and diazinon; and others) are toxic to both adults and larvae (Lee et al. 2008). These results suggest that other firefly species may also be sensitive to similar insecticides. In a field study to see how pretreating corn seed with a neonicotinoid called clothianidin affects insect communities, researchers identified declines in predator groups that included fireflies (Disque et al. 2018). Follow-up communication revealed that 70% fewer adult fireflies were captured in the treated plots compared to the untreated plots, likely due to clothianidin impacts on firefly larvae (Dively 2019, pers. comm.). Together, these studies suggest that common neonicotinoid and organophosphate insecticides cause direct harm to fireflies.

Though research on the direct impact of neonicotinoids and other insecticides on fireflies is sparse, studies of other beetle species can provide additional clues to potential firefly toxicity. Neonicotinoids—the most commonly used class of insecticide in the world—are broad spectrum, can persist in the environment for months to years, move readily in water, and are applied in both agricultural and residential settings. In agriculture, neonicotinoids can be applied to crops as seed coatings before they are planted or by spraying the crops during the growing season. This means that firefly larvae and burrowing adult females may be exposed to neonicotinoids through the soil. Mullin et al. (2005) found that carabid beetle species exposed to corn seedlings coated with field-relevant rates (i.e., realistic field dosage rates as might be used in routine applications) of several neonicotinoids (imidacloprid, thiamethoxam, and clothianidin) had nearly 100% mortality. Several beetle species also showed sublethal effects from contact with soil treated with imidacloprid (Pisa et al. 2015). In residential settings, neonicotinoids are commonly used to control white grubs (the larvae of various beetle species) in lawns. Application of imidacloprid to a lawn to target white grubs was found to reduce nontarget species, including beetles, by 50% or more over three years (Peck 2009). Some researchers suggest that treating rural lawns for white grubs has eliminated firefly populations from these habitats (Buschman 2019, pers. comm.).

Fireflies are closely related to click beetles (whose larvae are called wireworms), which can be agricultural pests. Neonicotinoids and other insecticides used to target wireworms are likely to be toxic to firefly larvae. One example is the pyrethroid tefluthrin, which is known to remain in soil and travel in runoff water from the application site (Whiting et al. 2014). Tefluthrin reduced the density of other beetles in a field study when it was applied to control wireworms (Babendreier et al. 2015).


Fireflies may be affected by pesticides used to treat closely related species, such as this wireworm, which is considered an agricultural pest. (Photograph: Katja Schulz, Flickr CC BY 2.0.)

Mosquito Management

Fireflies and mosquitoes often rely on the same habitats: humid areas with adequate moisture. Insecticide applications to manage adult mosquitoes (adulticides) may affect fireflies, especially because spraying is often done at dusk or at night. In one examination of beetle mortality from permethrin mosquito spraying, Peterson et al. (2016) observed acute mortality of the convergent lady beetle (*Hippodamia convergens*). While larvicides are often considered to have fewer off-target impacts than adulticides, care should be taken in firefly habitat because a common larvicide, methoprene, can also be toxic to some beetle species (Liu et al. 2016).

Impacts on Larval Food Sources

Firefly larvae eat soft-bodied invertebrates, including earthworms, snails, and slugs. Pesticide use that affects these prey species can influence larval firefly development. Earthworms are affected by neonicotinoid insecticides in a similar manner to insects—both groups share the same neural pathways disrupted by this class of insecticide (Pisa et al. 2015). Neonicotinoid toxicity to earthworms is particularly concerning because these chemicals can persist in many soil types for months to years (Wood and Goulson 2017). Through exposure to environmentally relevant concentrations in soil, neonicotinoids have also been shown to bioaccumulate and cause DNA damage in earthworms (Chevillot et al. 2017). Other common pesticides—organochlorines; pyrazoles; carbamates; the herbicide 2,4–D; and certain fungicides—are also toxic to earthworms (Correia and Moreira 2010; Wang et al. 2012). Insecticides may not directly affect slugs, but they can contaminate slugs through exposure. In one study looking at predaceous beetles that consume slugs, researchers found that slugs were unaffected by thiamethoxam but transmitted the insecticide to the beetles feeding on them, impairing or killing more than 60% of the beetles (Douglas et al. 2015). These results suggest that feeding on contaminated slugs could expose firefly larvae to pesticides. Similar issues could occur with snails, which can become contaminated with certain pesticides (Druart et al. 2011).

Fireflies can be exposed to pesticides through their prey. For example, larvae eat large amounts of soft-bodied invertebrates such as earthworms, which may bioaccumulate pesticides and pass them on to fireflies. (Photograph: Katja Schulz, Flickr CC BY 2.0.)

Climate Change

Our global climate is changing, causing shrinking glaciers, loss of sea ice, species range shifts, accelerated sea-level rise, and changes in phenology. In the United States and Canada, long-term predicted effects include rising temperatures, lengthening of the frost-free season, changes in precipitation patterns, increased drought and heat waves, and increased severity and frequency of storms and wildfires. Because climate is a key driver of insect species distributions and can influence their overall abundance, these factors are expected to have far-reaching impacts for many insect populations and the ecosystems upon which they rely (Stange and Ayres 2010). There is also evidence that extreme weather caused by climate change is likely to have implications for insect distribution in the coming decades. However, the combined effects of climate change and land use on invertebrates remain poorly understood (Forister et al. 2010). The magnitude of climate change will also play a role in determining how strongly insects are affected. A recent study by Warren et al. (2018) modeled the distributions of different taxa under various climate change scenarios. The study estimated that with climate warming of just 1.5°C above preindustrial levels, 6% of invertebrates could lose at least half of their range; at 2°C, this increased to 18% of invertebrates; and at 3.2°C, 49%.

A warming climate may lead fireflies to emerge earlier each spring, with unknown consequences for fireflies and the ecosystems of which they are a part. In one study on *Photinus pyralis* (shown here), researchers found that temperature was the primary driver of phenology. (Photograph: Katja Schulz, Flickr CC BY 2.0.)

Climate change can affect fireflies directly (for example, through habitat flooding or desiccation due to drought) or indirectly (through effects on their predators, competitors, and prey). Because firefly development depends on climate and local weather, environmental changes will likely affect their populations. A warming climate may cause overwintering larvae to emerge earlier in spring and could decrease development time for maturing adults (Lewis 2016a), with cascading effects that are not yet understood. In one study on the common eastern firefly (*Photinus pyralis*), researchers found that temperature was the primary driver of phenology, suggesting that climate warming may cause fireflies to become active earlier in spring; however, other climate extremes, such as changes in precipitation, may cause them to emerge later (Hermann et al. 2016). Records analyzed by Weston and Faust (2012) show that the synchronous firefly (*Photinus carolinus*) is emerging approximately one month earlier than the 15-year average. In another study using community science data from the program Firefly Watch, researchers found that certain variables—such as maximum winter and spring temperatures, as well as mean precipitation during the larval stage in the previous year—influenced adult firefly abundance (Evans et al. 2019). Higher temperatures may also shift species' ranges toward higher latitudes, with the southern portion of their ranges becoming unsuitable due to drought and other changes in precipitation patterns.

Some species may be especially vulnerable to climate change, given their habitat associations or life histories. For example, the Bethany Beach firefly (*Photuris bethaniensis*) and mystical lantern firefly (*P. mysticalampas*), two firefly species found along the mid-Atlantic coast, depend on coastal lowland freshwater habitats that are increasingly vulnerable to sea level rise as a result of climate change (Heckscher and Bartlett 2004; Heckscher 2013). Altered rainfall patterns can also affect already vulnerable populations. Buschman (2019, pers. comm.) notes that climate change is likely a threat for many species found in the West, as western populations tend to be small, isolated, and dependent upon permanent water sources. If these water sources dry up or otherwise disappear, it is unlikely that the population can persist. Furthermore, drought can directly affect not only fireflies, but also their moisture-dependent prey. At the other end of the spectrum, more frequent and severe flooding and storms can drown populations that depend on the land-water interface for egg laying and foraging.

Climate change is also leading to an increase in the frequency and intensity of wildfires, most notably in the western United States and Canada. Large, high-intensity wildfires have the potential to destroy small, isolated populations in areas already stressed by drought. However, wildfire pressures can be felt throughout North America. For example, in November 2016, a large wildfire erupted in Great Smoky Mountains National Park, which straddles the state line between North Carolina and Tennessee and is home to many firefly species, including the synchronous firefly (*Photinus carolinus*).

Tourism

Firefly ecotourism is relatively new in North America but growing quickly, especially in places with synchronous fireflies, such as the Great Smoky Mountains National Park. (Photographs: Great Smoky Mountains National Park, Flickr.)

Large congregating groups of synchronously flashing fireflies are a truly remarkable natural phenomenon, and one that understandably attracts a lot of interest from tourists. Firefly ecotourism plays a significant role in generating income for local communities throughout the world, including in Malaysia, Thailand, Taiwan, Japan, and Mexico. While firefly ecotourism is relatively new to the United States, places like Great Smoky Mountains National Park, which is home to the synchronous firefly (*Photinus carolinus*), have seen rapid increases in firefly-related visits. These increases in seasonal visitors may be a boon for the local economy but can be detrimental to firefly populations if not managed appropriately. Trampling of larvae and flightless females of co-occurring species, destruction of fragile microhabitats that support the fireflies, and increased light pollution have all been identified as threats associated with increased numbers of visitors. The Great Smoky Mountains National Park has become so popular with tourists during its annual light show that the park has implemented a lottery system to limit the number of visitors and protect the fireflies' habitat.

Introduced Species

Invasive insects, introduced nematodes, and other biological controls can pose direct threats to fireflies. The red imported fire ant, which can kill firefly larvae in the ground, may be partially responsible for declining firefly populations in the southern United States (Buschman 2019, pers. comm.). Biological controls such as the fungus *Beauveria bassiana* may also pose a new threat. Although this species of fungus is found naturally in low levels, it is now being cultured for use in soybean fields to control pests. Firefly researcher Lynn Faust observed large outbreaks of this fungus at one of her Tennessee field sites in 2015, killing thousands of invasive kudzu bugs and infecting some fireflies as well, including juvenile *Pyractomena borealis* and adult *Ellychnia corrusca* (Faust 2017, pers. comm.). While larvae of the invasive kudzu bug compete with firefly larvae for space and food, these high rates of infection and mortality are concerning, since the fungus also kills beetles and could have dramatic effects on local firefly populations. *Beauveria bassiana* is widely distributed and is documented to have a broad host range of over 700 insect species worldwide (Li 1987, cited in Goettel et al. 1990). Other biocontrol agents, such as predatory nematodes, may also pose threats to species already at risk, such as the microscopic *Steinernema* roundworm found infecting larvae of the rare Florida intertidal firefly (*Micronaspis floridana*) (Faust 2017, pers. comm.).

Invasive plants have the potential to severely threaten the long-term health of natural ecosystems, especially vulnerable habitats such as wetlands. Nearly a quarter of the world's most invasive plants are

Invasive plants such as the common reed (*Phragmites* sp.) have been identified as a threat to fireflies like *Pyractomena ecostata* that depend on brackish tidal marshes. *Phragmites* forms dense monocultures, displacing native plants and animals. (Photograph: Chesapeake Bay Program, Flickr CC BY-NC 2.0.)

wetland species, many of which form dense monocultures that crowd out native species, lower biodiversity, and alter ecological processes (Zedler and Kercher 2004). Because many firefly species depend on wetland and riparian habitats, these invasive plants can pose indirect threats to their populations by changing or eliminating firefly habitat. For example, invasive strains of the common reed (*Phragmites australis*) have been identified as a threat to the firefly *Pyractomena ecostata* that inhabits brackish tidal marsh areas along the Delaware and Florida coasts (Heckscher and Lloyd 2015). This reed outcompetes native salt marsh vegetation while providing little to no food or shelter for most native salt marsh–dependent species. Dense stands of invasive *Phragmites* can now be found across North America and are particularly dominant along the Atlantic coast. In the West, riparian firefly habitats may be invaded by species such as Japanese knotweed (*Polygonum cuspidatum*) and salt cedar (*Tamarix ramosissima*). Eastern broadleaf forests, another common firefly habitat type, are also heavily invaded by species such as kudzu (*Pueraria montana* var. *lobata*), garlic mustard (*Alliaria petiolata*), common buckthorn (*Rhamnus cathartica*), dame's rocket (*Hesperis matronalis*), and Chinese privet (*Ligustrum sinense*). Similar to wetland invaders, these species threaten native ecosystems by crowding out native plants and drastically altering the structure and function of the habitats they overcome. At the same time, nonnative plants may provide resources used by fireflies; careful site-specific assessments are needed to determine the role of these plants in the landscape and best practices for phasing out invasive species in favor of native plant communities. More research into how these nonnative invasive species affect fireflies is needed.

Commercial Harvesting and Overcollection

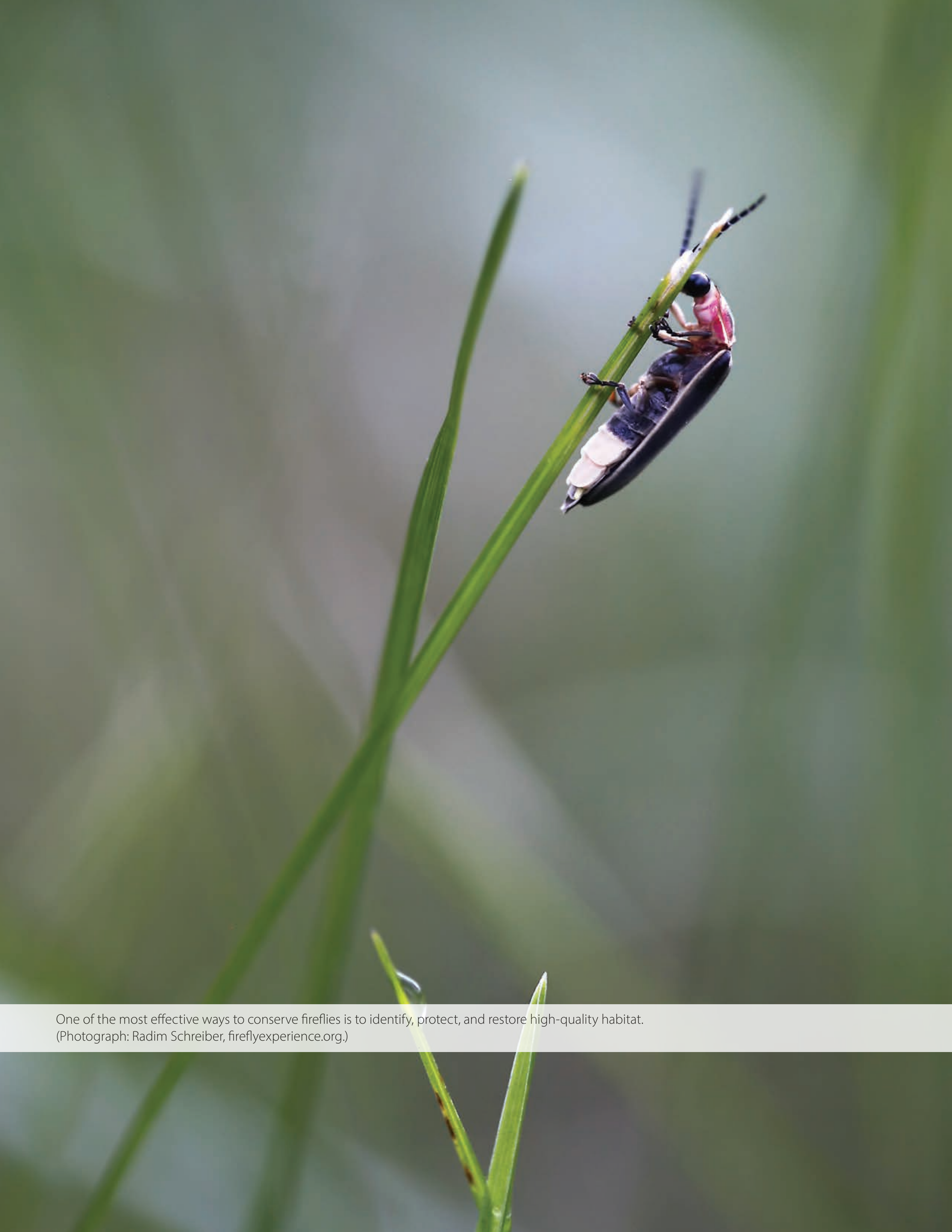
Around the world, wild fireflies have been collected and sold for use in celebrations, park beautification (through releases), and medical research. In the United States in particular, large quantities of fireflies were harvested commercially to extract luciferase for the biomedical industry (Bauer et al. 2013). In the 1960s, the American chemical company Sigma enlisted thousands of firefly collectors in dozens of states to collect fireflies for food-safety testing and research; more than 100 million fireflies were harvested (Lewis 2016a). By 1985, a synthetic version of these chemicals was available, eliminating the need for wild harvests, yet advertisements for collections have been found as recently as 2014 (Lewis 2016a). It is not fully known to what extent harvesting still occurs, and how such activities might affect firefly species. Bauer et al. (2013) developed population models in order to understand the combined effects of demography, harvest rate, delayed larval development, and unpredictable environmental fluctuations on population persistence of *Photinus* fireflies. Using a conservative estimate of population growth rates, they found that even moderate rates of annual harvest were likely to cause a firefly population to go extinct within 50 years.

Other Threats

Small, isolated populations, such as those associated with flashing species in western North America, are also extremely vulnerable to random weather events, and are generally at greater risk of local extinction from normal population fluctuations due to predation, disease, and changing food supply. Periodic natural events such as floods, hurricanes, or droughts can further stress these populations. In addition, they can experience a loss of genetic variability and reduced fitness due to inbreeding that can occur in small, fragmented populations. Both wildland and prescribed fires may also be affecting firefly populations. Lloyd (2018) observes that prescribed fires for forest management may have negative impacts on arboreal species such as *Pyractomena*; natural fires tend to occur after pupation, but burns conducted earlier in the season could kill pupating *Pyractomena* found low on tree trunks and stems.

Certain life-history traits may make some firefly species more vulnerable to threats than others. For example, arboreal species such as this pupal *Pyractomena* are more vulnerable to desiccation, fires, and predation. (Photograph: Joe Walewski / iNaturalist CC BY-NC.)

Regional and local declines in terrestrial mollusks may further affect firefly larvae, which rely on soft-bodied snails and slugs (as well as earthworms and other invertebrates) for food. Nonmarine mollusks (freshwater and terrestrial species) are among the most imperiled animals on our planet. This group has the highest number of documented extinctions of any major taxonomic group in the world; 42% of the 693 recorded extinctions of animal species between the years 1500 and 2003 are mollusks (Lydeard et al. 2004). Régnier et al. (2009) document an astonishing 566 mollusk species and subspecies (including marine) extinctions since 1500. Actual numbers of extinctions are likely higher, given the relatively little research and conservation attention that invertebrates receive and the fact that many species remain undescribed or unknown to science.



One of the most effective ways to conserve fireflies is to identify, protect, and restore high-quality habitat. (Photograph: Radim Schreiber, fireflyexperience.org.)

4

Conservation Guidelines

Most firefly researchers agree that habitat loss and degradation, in addition to light pollution, pesticide use, and climate change, are the leading threats to fireflies in the United States and Canada (Lewis et al. 2019). Some of the most effective strategies for conserving fireflies include identifying, protecting, and restoring high-quality habitat for these species. The following guidelines are meant to help the general public as well as managers of parks and other natural areas to incorporate practices that can help fireflies and the habitats they depend upon. We also provide recommendations for taking action within your community and educating others about the wonder of fireflies and why we should all work toward their conservation.

Surveying and Monitoring Fireflies

Since the locations where fireflies occur are not always well documented, identifying species' distributions and their habitats is a key first step to conserving these animals. Prior to any habitat enhancement or management activities, you should undertake a firefly inventory to establish the presence or absence of fireflies at known and potential sites. Inventory and monitoring are critical for understanding population trends and impacts of threats and management activities. Yet baseline data for many species are lacking, and long-term monitoring of populations across a broad geographical scale is limited. One of the reasons for this is the fact that fireflies often have short breeding seasons and may only flash for a brief period each night. In addition, identification for many species depends on flash behavior and small anatomical details. Until very recently, field guides were not available for fireflies, but new publications (see Appendix B) are helping to break down some of these barriers.

We encourage anyone interested in creating, protecting, or restoring habitat to first understand what species exist in a particular area, which can help guide the conservation actions you take. To get an idea of what species occur in your area, use the map of research-grade firefly observations collected through the Fireflyers International Network's project on iNaturalist, which collates firefly observations throughout the United States and Canada. As you begin to make your own firefly observations, you can contribute to this growing body of knowledge. A relatively simple but scientifically meaningful way to do this is to participate in established community science programs and crowdsourcing forums such as iNaturalist. Community science has proven to be very useful for tracking species of concern across a large geographic area, and a number of programs are now underway to help address data gaps in the firefly world. For the most part, all you need are a camera or smartphone and a few notes on location, habitat, and flash patterns in order to participate. A good option for opportunistic sightings and for reporting observations of nonflashing individuals is iNaturalist. For firefly enthusiasts who want the option to contribute more in-depth data on flashing species, we recommend using a dedicated firefly community science program, such as the Firefly Watch program run by Mass Audubon. This program uses data gathered by community scientists to track firefly occurrences across North America. You can contribute to it by monitoring fireflies in your own yard or a nearby natural area.

Fireflies need four basic things: food, shelter, moisture, and places that are safe from pesticides. Native plants can provide some of these features. (Photographs: left, Xerces Society / Sarah Foltz Jordan; center, Xerces Society / Jennifer Hopwood; right, Katja Schulz, Flickr CC BY 2.0.)

Creating, Restoring, and Protecting High-Quality Habitat

Basic Needs

In general, all fireflies require four basic things: food, shelter, moisture, and protection from pesticides. Individual species will have more specific habitat or food requirements, but by keeping these requirements in mind, you can easily provide for fireflies in your yard, park, or natural area. In particular, most fireflies need:

- abundant larval food sources, including soft-bodied invertebrates such as snails, slugs, and earthworms;
- safe places to overwinter, including trees, leaf litter, and underground burrows;
- clean sources of water or moisture so larvae and their prey do not desiccate;
- protection from pesticides—especially insecticides;
- undisturbed ground for burrowing larvae and flightless adult females;
- native vegetation of varying heights (so that adults have places to perch or take shelter); and
- dark nights, for dusk- and night-active species that use bioluminescent light signals to communicate and mate.

Some species also need:

- food sources for species that feed as adults, including tree sap, flower nectar, and other fireflies (e.g., *Photuris* females often eat other species of fireflies, such as those in the *Photinus* genus), and
- healthy populations of ant associates for larval and adult female *Pleotomodes* and *Prolutacea* species that live in ant nests.

Recommendations

Habitat Protection

The easiest way to help fireflies is to identify and protect the habitat they already use. Depending on where you live, this may be an old field, suburban lawn, nearby wetland, wooded riparian area, or local park. Within these areas, it is important to hone in on microhabitats used by fireflies. This can include downed wood (rotting logs) used by overwintering larvae, naturally occurring mosses that females may use to lay eggs, and large-diameter trees with furrowed bark used by species that overwinter in these crevices. For example, eastern *Pyractomena borealis* fireflies, which pupate in tree bark furrows and emerge early in the year, often use the same large-diameter tulip poplars, hickories, and oaks year after year (Faust 2017). Adults of the common day-active winter firefly (*Ellychnia corrusca*) also appear to prefer tree species with more deeply furrowed bark, and they can be found in loose colonies on these tree species as well (Faust 2012; Deyrup et al. 2017). Consider leaving some areas of your yard or property a little unkempt or more natural—the perimeter can work well for this if you want to keep wild areas to the edges. For sites with known populations of imperiled species, you may want to hire an expert consultant to work with you on best approaches for that particular species.

Ground-Disturbing Activities

Females of many species and all larvae spend most, if not all, of their lives at ground level. Ground-disturbing activities such as raking, mowing, brush hogging, and thatch removal can negatively influence fireflies during these vulnerable life stages by removing needed microhabitat features or directly causing mortality. To protect fireflies, consider the following:

- Leave the leaves. Leaf litter can provide shelter for fireflies and improve the moisture content of soil, which can in turn attract firefly food sources. Refrain from raking or leaf blowing so fireflies and their prey can have protected places to live. Consider using fallen leaves in place of wood mulch.
- Mow less often. Mower blades and ground trampling can directly kill fireflies, as both larvae and egg-laying females spend most of their time on the ground, and adult males use grasses and forbs as resting places. Allowing the grass to grow higher provides fireflies with more places to hide and find shelter. If you do have to mow, consider setting your mower height higher to leave a buffer between fireflies and the mower blade.
- Use fencing or other exclusions to keep cattle and other animals from destroying fragile wetland habitats used by fireflies.
- If ground-disturbing activities must occur, conduct them on a rotational basis. Avoid disturbing an entire habitat patch, and instead rotate activities so that no more than a third of the habitat is disturbed in any given year. Consider conducting these activities when larvae and flightless females are dormant, which for many species is over winter.

Top: Although *Pyractomena* larvae like the one pictured here are typically found on trees, other firefly larvae and flightless females use leaf litter for shelter, mating, or hunting for prey. Bottom: Even small patches of habitat can provide a place for fireflies to perch or shelter. (Photographs: top, Xerces Society / Sarah Foltz Jordan; bottom, Xerces Society / Jennifer Hopwood.)

Pesticides and Other Chemical Contaminants

Pesticides, including insecticides and herbicides, have the potential to kill fireflies or indirectly harm them by removing or degrading important habitat features and prey.

- Eliminate all cosmetic or unnecessary pesticide use that is not responding to economic damage or a public health risk. Address pests with an integrated pest management plan that prioritizes cultural control, with pesticide use as a last resort. If pesticides are used, work to minimize impacts to fireflies and their habitat.
- Reduce or eliminate pesticide use that can kill fireflies or their prey, or alter their habitat.
    - Avoid broad-spectrum insecticide use, including all neonicotinoids, in and around firefly habitat.
    - Minimize herbicide use in firefly habitat to avoid potential negative impacts.
- Create an integrated mosquito-management plan. Such plans all include the same core components: personal protection, monitoring and surveillance, removal of artificial breeding habitat, and early intervention. You should only consider insecticides to reduce adult mosquitoes during a disease outbreak, and use them as a last resort in a manner that is as targeted as possible. Guidance on effective mosquito management is available from Xerces at https://xerces.org/pesticides/effective-mosquito-management.
- Do not use chemical fertilizers on lawns, especially ammonia-based products. These add salts to the soil, which can negatively affect soil-dwelling slugs, snails, and worms—the primary food source for firefly larvae.
- Allow slugs and snails to persist, as these are important food sources for many firefly species. When possible, refrain from using slug baits or other molluscicides that may jeopardize larval food sources.

Other Pest-Management Activities

- Avoid tree banding on species used for pupation and overwintering. Tree bands are sticky wraps placed about three feet off the ground to trap pests that crawl up and down tree trunks and lay their eggs in the canopy. These bands can trap and kill nontarget species such as fireflies.

Invasive Plants

- Have a scouting and monitoring program to identify and control invasive weeds before they overwhelm a site.

Light Pollution

Artificial light alters the behaviors and reproductive success of many nocturnal animals (Gaston et al. 2015). For example, fireflies in light-polluted habitats have trouble locating potential mates (Owens and Lewis 2018). Being thoughtful about outdoor lighting will benefit not only fireflies but other nocturnal animals as well.

- First, reduce or eliminate unnecessary outdoor lighting, such as security floodlights, especially in summer when adult fireflies are active. Keep as many areas as possible dark at night.
- In areas where lights cannot be turned off at night, consider the following:
    - Swap bright light bulbs for dim red bulbs, which fireflies are less able to see, or filter existing bulbs to make them dimmer and redder.
    - Limit illumination to desired areas, such as sidewalks or pathways.
        - Place landscape lighting low to the ground to reduce the lit area.
        - Shield lights so they point down, not out 360 degrees.

- Use motion-detection or automatic timers so lights are on only as needed.
- Limit the number of hours per day that lights are on.

- Close curtains or blinds at night in order to reduce the amount of light that shines outward from your windows.

Public Access and Ecotourism

Firefly viewing is a beloved pastime for adults and children alike. While your effect on fireflies and their habitats are likely minimal during a typical evening show in your yard, trampling can be a major threat to relatively immobile larvae and flightless females in areas that get more human traffic. In parks and other natural areas, protect occupied firefly habitat by using physical barriers and limiting foot traffic to designated pathways.

Firefly ecotourism is growing in the United States, especially in places that host synchronous fireflies. While firefly ecotourism can benefit local economies and expose more people to the wonder of fireflies, it also comes with management challenges. Firefly ecotourism may be in its infancy in North America, but we can learn from other regions where this type of tourism has been occurring for decades, most notably in many Asian countries. Consider these guidelines for implementing sustainable tourism programs in areas with high firefly interest:

- Regulate the number of visitors to a site to minimize impacts to firefly populations.
- Restrict visitors to clearly marked paths and viewing areas, keeping core habitat behind protective barriers. Use raised boardwalks and platforms to avoid trampling of adult females and larvae.
- Adopt best practices (such as signage, public education, and equipment clean-off sites) to reduce weed seed introductions via visitors' clothing and vehicles.
- Do not allow the use of flash photography, cell phones, or other lights like headlamps or flashlights that could disrupt firefly courtship.

Box 1: Apply Your Own Light Filter

Changing the color of your outdoor lighting can help reduce its impact on light-sensitive firefly species. But this doesn't mean you have to replace every bulb—it is much easier and cheaper to alter the color of your house lights, path lights, or other light sources with gel filters. Laboratory trials have shown that stacking four layers of red filter on a standard white LED flashlight bulb effectively eliminates harmful short wavelengths (i.e., blue and green light that interferes with firefly communication) while also lowering overall light intensity, making a filtered white LED flashlight bulb even better than an unfiltered, ultra-bright red LED flashlight bulb of the same make and model (Owens 2019, unpublished data). What's more, the light created by these filters is easier on human eyes and less likely to bounce around the atmosphere—improving your view of stars and flashing fireflies alike.

Being thoughtful about protecting fireflies while still enabling public access is an important part of sustainable ecotourism. (Image: Great Smoky Mountains National Park, Flickr.)

- Educate visitors and community members about firefly ecology and conservation needs through the use of informational signs, brochures, or local workshops and lectures.
- Include the community in decision-making regarding firefly ecotourism and seek support for policies that will benefit fireflies, such as dark-sky initiatives.
- Employ and train knowledgeable guides to lead educational tours and be on hand during the active firefly season.
- Explore opportunities for engaging visitors and the community through interactive exhibits, art-based media, and community science programs, such as Firefly Watch.

Habitat Creation and Restoration

Habitat loss has been identified as one of the greatest threats to fireflies. You can help alleviate this threat by restoring an area where they once persisted or creating a link between occupied habitats. In addition to the recommendations listed in the Habitat Protection section, consider the following when creating or restoring your firefly habitat.

Choosing a Restoration Site
Consider the basic needs of fireflies and determine whether your site is or can be made suitable for fireflies. There are a few factors to evaluate.

- Firefly presence: Evaluate the baseline firefly community to understand if they are present in your site. Do fireflies currently inhabit the site, or have they in the past? Will restoring this site link existing populations? Fireflies do not disperse very far, so keep in mind that newly created or restored sites may not immediately attract fireflies if they are not already present in your area.
- Water availability: One of the most important factors is the availability of moisture, which most firefly species and their prey need. Does your site have a perennial water source or moist, shady places that can support fireflies? If not, can you create a water source (e.g., a small pond or water feature)?
- Distance from artificial light sources: Dark nights are important for many species of fireflies. Is your restoration site adjacent to an area that is lit at night? If so, are there steps you can take to mitigate light pollution?
- Distance from agricultural fields: While fireflies can be found in abundance in some agricultural areas, consider potential pesticide use and associated drift before restoring or creating sites adjacent to these areas.
- Presence of invasive plants: Invasive plants can have negative effects on native communities, but they may also provide important structural elements to species like fireflies. Are invasive plants present at your site? If so, identify replacement native plants that have similar structural value to the nonnative species and develop a restoration plan that reduces the impact of habitat conversion on fireflies by restoring only a third of the site in any given season.
- Habitat types: Fireflies are often associated with moist sites, such as wet meadows, riparian areas, and woodlands, although they can be found in a large variety of habitats, from old fields and urban lots to desert canyons and mangrove swamps. If possible, determine which species naturally occur in your county or region and focus on providing habitats those species are known to use.

Plant-Selection Considerations
Fireflies use plants of varying heights and structures for courtship, shelter, foraging, egg laying, and pupation. Plants can also help retain soil moisture, which is critically important to most firefly species.

You can ensure that some areas of your environment stay moist year-round by creating shady habitats with a diversity of native plants. When considering plants to include in your firefly habitat, keep in mind that site heterogeneity (i.e., a diversity of microhabitats) is important to providing habitat for a variety of firefly species.

- Grasses: Tall grasses provide cover for larvae and their prey. They can also give female fireflies a better vantage point at night, when they crawl up to watch for males flashing overhead.
- Flowering forbs: Although most adult fireflies do not feed, there are some reports of adults visiting flowers. In Massachusetts, adults of the winter firefly (*Ellychnia corrusca*) have been observed feeding on the nectar of aster and goldenrod flowers (Rooney and Lewis 2000). Adults of some species may also nectar on common milkweed (*Asclepias syriaca*) (Faust and Faust 2014). Providing a diversity of flowering plants throughout the growing season may benefit fireflies and can also increase the diversity of pollinators and other wildlife at your site.
- Shrubs: Brushy areas provide shelter and perches for fireflies, and they increase the diversity of vegetation heights available to them.
- Trees: Tall trees adjacent to or within habitat can provide shade and shelter as well as mating display perches for species that signal from the canopy. Tree branches can also help block light pollution, increasing the darkness needed for bioluminescent communication. Consider using trees to increase edge habitat, which occurs at the boundary between two habitat types and is favored by some firefly species.
    - Pine trees are commonly associated with firefly habitats in the East. Their fallen needles provide great habitat for firefly larvae and adult females, and their dense branches can help block light pollution.

Case Study

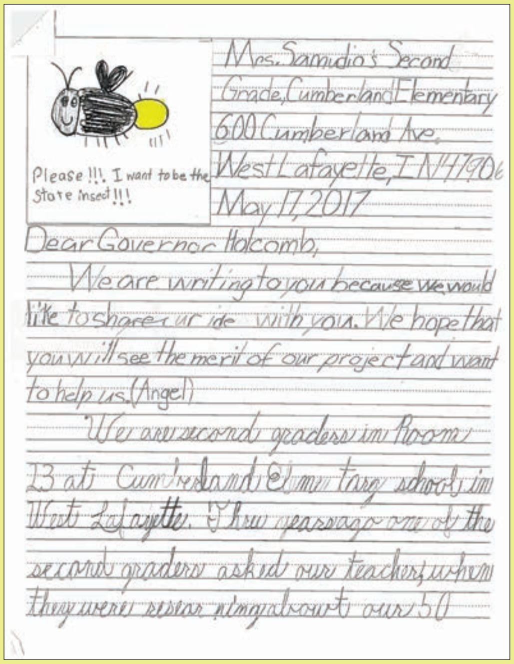
Photograph: Justin Meissen, Flickr CC BY-SA 2.0.

Wet Meadow Restoration in Suburban Minnesota

Private and public entities alike can undertake restoration to improve firefly habitat. On a two-acre residential lot just outside of Minneapolis, a homeowner has launched a multiyear meadow- and landscape-restoration project to support insects and other wildlife. The lot consists of a small wetland and some upland turf areas and hosts a large firefly population. It also hosts a complex tapestry of invasive plants dominated by reed canary grass (*Phalaris arundinacea*). Although restoration efforts were not initiated to target fireflies specifically, careful consideration of fireflies within the larger community has had positive effects.

There are two primary aspects to this project: The first and longest-term effort has been to install plugs of desirable plant species into the wetland (among the reed canary grass) and then spot treat the invasive grasses in an attempt to slowly open space for the desirable species to spread. Second, the homeowner is slowly replacing areas of mowed turf and nonnative ornamental landscape plants with native prairie species. These efforts combined, the goal is to slowly expand natural habitat and squeeze out the nonnative plants.

This approach has complementary benefits for both the landowner and fireflies. For one, it does not create a large, area-wide disturbance that might harm the local firefly population or other wildlife. Because the homeowner is restoring a little bit at a time, the fireflies can colonize the restored native plant areas while the areas dominated by reed canary grass and turf become smaller and smaller. And second, the multiyear approach is less prohibitive in terms of cost and labor time for the landowner. It is a simple model that other homeowners and managers of smaller properties can replicate.



Please !!! I want to be the state insect !!!

Mrs. Samudio's Second Grade, Cumberland Elementary
600 Cumberland Ave.
West Lafayette, IN 47906
May 17, 2017

Dear Governor Holcomb,

We are writing to you because we would like to share ur ide with you. We hope that you will see the merit of our project and want to help us. (Angel)

We are second graders in Room 13 at Cumberland Elementary school in West Lafayette. Three years ago one of the second graders asked our teacher, when they were researching about our 50

This letter to Indiana's governor, part of a successful campaign to nominate a state insect, was written by second graders at Cumberland Elementary School. (Image: courtesy Maggie Samudio.)

Box 2: Say's Firefly Becomes Indiana's State Insect after Years of Lobbying by Students

When second grader Kayla Xu discovered that her state of Indiana did not have a designated state insect, she quickly set about changing the situation. Settling on the Say's firefly (*Pyractomena angulata*), Xu rallied fellow classmates and teachers at Cumberland Elementary School to lobby lawmakers to introduce legislation that would lead to an official designation. That designation came four years later, in February 2018, when the Say's firefly was officially named Indiana's state insect. The firefly was first described by Thomas Say of New Harmony, Indiana, who has often been called the father of American entomology.

- The winter firefly (*Ellychnia corrusca*) overwinters as an adult in deeply furrowed bark of large trees (Faust 2012). Eastern *Pyractomena borealis* fireflies seek out bark furrows for pupation, often using the same large-diameter tulip poplars, hickories, and oaks year after year (Faust 2017).
- Maple trees may provide a secondary moisture source to fireflies. *Ellychnia corrusca* adults have been observed feeding on the sap and floral nectaries of nonnative Norway maple (*Acer platanoides*) in Massachusetts (Rooney and Lewis 2000); native maples may be used as well.

Other Considerations

Firefly larvae and pupae generally seek shelter in moist soil, leaf litter, or rock crevices. Adult females seek out similar places for egg laying, often using moist soil, moss, rotten logs, and the bases of bunch grasses. These microhabitats tend to attract snails, slugs, and earthworms as well—key components of a larval firefly's diet. Ensuring these habitat components are available will help maintain a healthy firefly community.

Additional Guidance

There is a plethora of guidance available on wetland and native plant restoration and site prep. While such guides do not focus on fireflies, creating and restoring functional native ecosystems can have far-reaching positive impacts on fireflies, especially if the recommendations in these guidelines are taken into consideration. Land owners seeking additional guidance can also reach out to their local conservation districts. Often referred to as soil and water conservation districts, these agencies provide technical assistance and tools to manage and protect land and water resources in the United States and Canada.

Advocacy and Outreach

Fireflies are well loved by the public. However, despite concerns about potential population declines, they have received relatively little conservation attention. You can help initiate this important conversation by advocating for fireflies in your community. People generally want to ensure that fireflies continue to persist into the future, but they may not know what fireflies need or what they can do to help.

- Set up an educational event, work party, or festival to celebrate World Firefly Day, which takes place every year on the first weekend in July.
- Enlist neighbors in your efforts to make your community more firefly friendly. Encourage the creation of firefly-friendly habitats, and talk to neighbors about changing their lighting habits.
- Educate tourists and local residents about the significance and diversity of fireflies.
- Share information about common local species, their flash patterns, and ways to contribute to firefly conservation with your family, friends, and coworkers.
- Incorporate firefly biology and conservation needs into school curricula.
- Participate in community science efforts like Firefly Watch, the Fireflyers International Network's iNaturalist project, or regional initiatives. Encourage your friends and family to do the same.
- Identify areas where fireflies occur in your neighborhood or region and, if possible, note any rare or imperiled species. Become a steward of the habitats that rare fireflies need, and ensure they are protected from development and other threats.
- Work with local, state, and national conservation organizations to establish firefly sanctuaries.
- Work with your local parks department to protect and restore small pockets of undisturbed habitats in urban areas, such as those found in local parks, cemeteries, and other natural areas.
- Join or start a local chapter of the International Dark-Sky Association to advocate for local policies to control light pollution. In addition to helping fireflies and allowing people to appreciate the night sky, these initiatives often result in cost savings for municipalities and businesses.
- Determine if your community is eligible for designation under the International Dark Sky Places Program; if so, work with leaders to apply.
- Work with your municipality to pass pesticide policies that are friendly to fireflies and other beneficial insects, such as native pollinators.

Research Needs

Despite fireflies being well-studied organisms in regards to their evolution, reproduction, and mating behavior (with an emphasis on bioluminescence), relatively little is known about the life history of many firefly species and their population trends. Few studies have been conducted on a broad scale to investigate larger questions about firefly ecology, impacts of land-use changes, or conservation strategies. These knowledge gaps could guide further research studies:

- specific larval diet of individual species;
- life-history traits and habitat needs or associations of individual species;
- species distributions, particularly in the West;
- species population sizes and trends;
- status and extent of declines, if applicable;
- direct and indirect effects of pesticides on fireflies; and
- direct and indirect effects of other threats on fireflies, including artificial light at night, climate change, and invasive species.

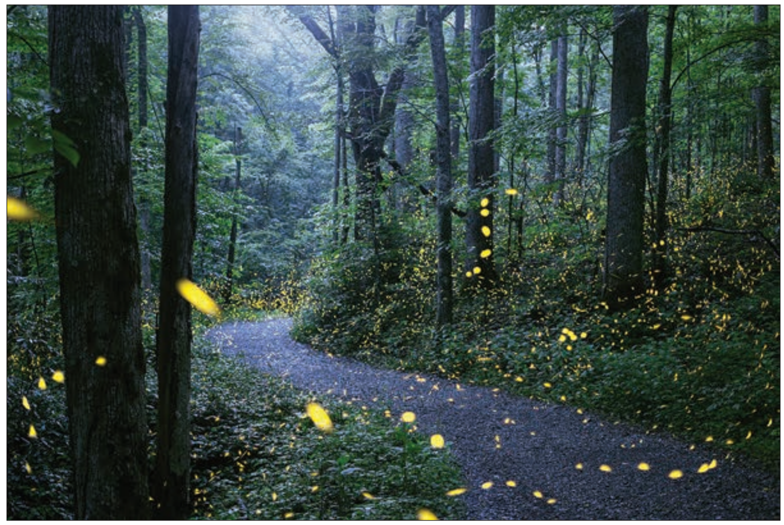
Fireflies are critical components of our natural and cultural heritage. (Photograph: Xerces Society / Sarah Foltz Jordan.)

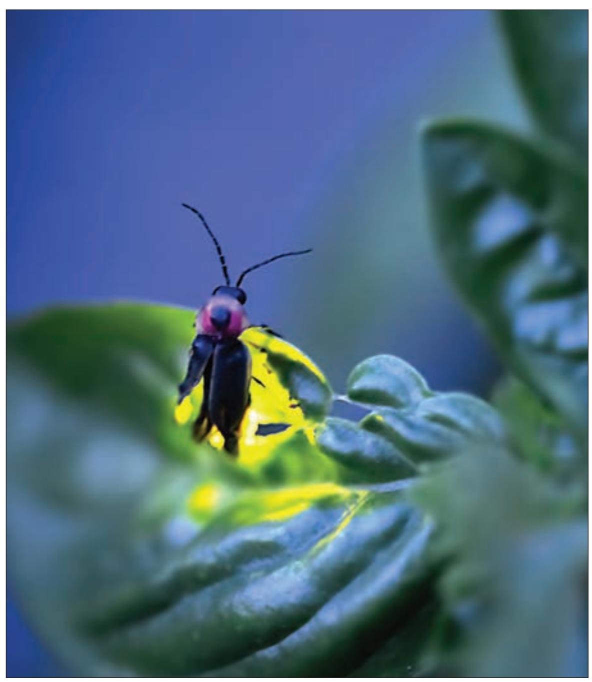
5

Conclusions

Fireflies are part of our cultural and biological heritage. They provide important ecosystem services, have played major roles in biomedical research, and support local economies through tourism dollars. Because so many of us cannot imagine future generations inheriting a world without fireflies, they make ideal flagship species for conservation (their sensitivity to light pollution and wetland degradation also can make them important bioindicators). Despite the importance and public support for fireflies, a growing number of anecdotal reports point to firefly declines, and many firefly researchers have expressed concerns about local extinctions. While habitat loss and degradation likely pose the greatest threats to firefly populations, light pollution, pesticide use, climate change, and introduced species undoubtedly play roles as well.

Creating and restoring habitat, advocating for firefly protection, and building sustainable ecotourism industries around existing populations are some of the best ways to conserve firefly populations. Everyone can contribute to firefly conservation, whether you are a homeowner who sets aside a small refuge on your property, a land manager who changes grazing practices to protect wetland habitat, or an advocate who works with your municipality to change public lighting to be more firefly friendly. We hope these guidelines will provide the information you need to consider fireflies, learn more about them, and share what you know with others. Together, we can ensure that fireflies persist for generations to come.





Can you imagine a world without fireflies?
(Photographs: Radim Schreiber, fireflyexperience.org.)

Appendix A:
Guide to Native Firefly Genera

Nearly 170 native firefly species have been described from the United States and Canada, representing 20 genera. More species and genera are described each year. In 2018 and 2019 alone, 37 new species were described from the United States (Lloyd 2018; Faust and Davis 2019). In addition to native fauna, a nonnative species, *Phosphaenus hemipterus*, is also in North America. In the 1950s, a single specimen from Europe was discovered in Nova Scotia, presumably arriving in ship ballast around 1800 (Arnett et al. 2002). The species is now more widespread and has been reported in at least three Canadian provinces (Luk et al. 2011; Majka 2012). Firefly genera can be classified by their primary form of communication—flashing or flickering, glowing, or chemical pheromones. This guide lists the most commonly encountered genera first.

Flashing Fireflies

Our best-known, and arguably most-beloved, fireflies use quick, bright flashes to find and attract mates. The majority of these species occur east of the Rocky Mountains, although some small, isolated pockets of flashing fireflies occur in damp habitats west of the Rockies as well. More than 100 species of flashing fireflies have been described from the United States and Canada. Males emit flashing or flickering patterns to attract the attention of females that respond from the ground or from perches on foliage.

Photuris

This is one of the most common flashing genera of fireflies, with most species communicating with greenish light. *Photuris* is a large genus with more than 60 described species; 37 of these were described in 2018 and 2019 alone (Lloyd 2018; Faust and Davis 2019). As a group, they are generally easy to distinguish from other fireflies, given their humpbacked appearance and long legs (Lewis 2016a). At the species level, however, things get much more confusing. Each species has a wide array of flash patterns that it can employ, making it difficult to identify species based on their signals alone (Lewis 2016a). In addition, many female *Photuris* are specialist predators of other fireflies and may mimic the flash patterns of other species to attract males and eat them. Add to that the fact that the genitalia of nearly all *Photuris* look almost identical (usually a defining

Photuris species are easily distinguished by their humpbacked appearance and long legs. (Photograph: Katja Schulz, Flickr CC BY 2.0.)

characteristic of a species), and it is no wonder that longtime experts have difficulty telling them apart. *Photuris* fireflies can be found in many different habitats, including tree margins and damp openings (Faust 2017), and their range spans eastern North America to the southern Rocky Mountains. Their larvae pupate underground.

Photinus

Photinus fireflies are common and widespread from the East Coast to Colorado and Texas and can be found in a variety of habitats, from lawns and marshes to forests and riparian wetlands (Faust 2017). Thirty-four species have been described from the United States and Canada, with activity periods that range from dusk to full dark. The best-known *Photinus* species is likely *P. pyralis*—the common eastern firefly or big dipper firefly—that flies at dusk on summer evenings. This genus includes two species with nonluminous adults, *P. indictus* and *P. cookii*. Larvae pupate underground.

Pyractomena

Fireflies from another common but less frequently encountered genus, *Pyractomena*, have an orange or yellow flash. Sixteen species of *Pyractomena* have been described. They can often be found in treetops or in marshes and boggy areas (Faust 2017). Larvae crawl up vegetation to pupate, which may be an adaptation to survive areas that frequently flood. In some species, larvae can be semi-aquatic, hunting for food both above and below the water line (Lewis 2016a). *P. borealis* are among the first fireflies to emerge in spring and can be seen as early as February in southern states like Florida (Lewis 2016a). They can be found across North America with the exception of the southwestern United States, but populations west of Kansas are scattered.

Photinus (top) and *Pyractomena* (bottom) fireflies are relatively common in the central and eastern regions of the United States and Canada. (Photographs: top, Katja Schulz, Flickr CC BY 2.0; bottom, Whitney Cranshaw, Colorado State University, Bugwood.org CC BY 3.0 US.)

Bicellonycha

This little-known genus is represented by a single species, *Bicellonycha wickershamorum*, and two subspecies, all of which are known from Arizona at elevations from 4,000 to 6,000 feet. Adults of these fireflies are active in spring, from late May to June. They can sometimes occur in large numbers in marshy areas along permanent streams (Buschman 2016).

Micronaspis

Only one species has been described from this genus, the dark-active Florida intertidal firefly (*Micronaspis floridana*). This species is known only from salt marshes and mangroves along coastal regions of Florida and some northern islands of the Bahamas (Faust 2017). It is considered highly threatened and uncommon, with declines in its mangrove habitats likely contributing to its rarity. Hurricanes can pose a threat to this species, although larvae are able to float like little boats, which may aid their survival (Faust 2017, pers. comm.). *Micronaspis* fireflies have a yellow flash (Faust 2017).

Aspisoma

Typically a tropical genus, *Aspisoma* has only one species recorded in the United States—*A. ignitum*, known from both Florida and Texas. Relatively little is known about this species, and in Texas it has not been seen since the 1970s (Pfeiffer 2019, pers. comm.). This firefly is dependent on groundwater seeps that occur in sand dunes, which have been disappearing in recent decades, especially since the onset of the fracking boom in Texas (Pfeiffer 2019, pers. comm.).

Bicellonycha is a little-known genus. Only a single species from *Micronaspis* and *Aspisoma* are known from the United States. From top: *Bicellonycha wickershamorum, Micronaspis floridana* (adult and larva), and *Aspisoma ignitum*. (Photographs: top, Kyle Schnepp; second, Drew Fulton; third, Ted C. MacRae; bottom, magichin, iNaturalist CC BY-NC-ND 4.0.)

Glow-Worms

Glow-worms, like flashing fireflies, are active at dusk or after dark and use bioluminescence to communicate. Unlike flashing fireflies, their communication occurs with glowing light. Adult female glow-worms cannot fly, and their wingless bodies superficially resemble larvae rather than the typical adult body form (hence the name glow-worm). Females are bioluminescent, and males (which may or may not be bioluminescent) have evolved very large eyes with which to locate glowing females. Glow-worms are more commonly found in the West. Relatively little research has been conducted on glow-worms in the United States and Canada and, as a result, our knowledge of their life history, distributions, and behavior is limited.

Phausis

Phausis includes the most firefly species of glow-worm genera in the United States and Canada, with 10 described. Females glow, whereas most *Phausis* males are dark; males of the blue ghost firefly (*P. reticulata*) are a well-known exception to this (De Cock et al. 2014). *Phausis* can be found widely distributed across the United States and Canada, from Florida to British Columbia. The most famous species is undoubtedly *P. reticulata*. Sites that host these otherworldly blue ghosts are increasingly popular ecotourist attractions, drawing visitors to a beautiful evening spectacle: glowing males slowly flying over the forest floor as they search for dimly glowing females. Females of all *Phausis* species are vulnerable to trampling and other activities that directly affect their home sites.

Pleotomus

Pleotomus glow-worms are rare but widespread (Faust 2017), found from Tennessee to the Great Plains and west to California. Females have large light organs near the tail; males may also glow when young because of larval light organs (Buschman 2016), but they are generally dark as adults. All three of the described species in this genus are thought to use pheromones in addition to bioluminescence to communicate (Lewis and Cratsley 2008). This genus is poorly understood. Two of the species, *P. nigripennis* and *P. pallens*, are usually collected at blacklight traps (Faust 2017) and are attracted to street lamps and other light sources, which can make them more vulnerable to light pollution (Pfeiffer 2019, pers. comm.).

Phausis reticulata (top) is well known in the East. Other glow-worms, such as *Pleotomus* (center and bottom), are much less studied. The firefly at center is an adult male, while the firefly at bottom is a flightless female (note her tiny black wing covers). (Photographs: top, John Abbott; center, Robby Deans, iNaturalist CC BY-NC 4.0; bottom, Joe Cicero.)

Microphotus

All seven *Microphotus* glow-worm species are restricted to the southwestern United States and Texas. As is typical of most glow-worms, females may travel only a few centimeters from their home site in their lifetime (Cicero 1981). Unlike many other glow-worms, both males and females glow. Females of *M. dilatatus* have been observed using a variety of sites to shelter from daytime temperature extremes, including abandoned spider, ant, and rodent burrows (Cicero 1981). Females of another species, *M. pecosensis*, may use specific rocks as their retreats, along high streambanks in mixed conifer woodlands (Cicero 1981).

Pleotomodes

Only two species of the unusual genus *Pleotomodes* are known from the United States, found in Florida and the southwestern United States. Both adult females and their larvae live in ant nests. Females, larvae, and pupae all glow (Sivinski et al. 1998); males may also glow, but weakly (Faust 2017). Because of their secretive lifestyles, little is known about these species' diets or general life histories, although Lloyd (2018) has speculated that they eat the food or young of ants, or even other ant nest inhabitants. *P. needhami*, which has been studied at the Archbold Biological Station in Florida, appears to be dependent on two or three ant species, including the fungus-growing species *Trachymyrmex septentrionalis* and the carnivorous *Odontomachus clarus* (Sivinski et al. 1998).

Prolutacea

Similar to *Pleotomodes*, *Prolutacea*, with its single species, *P. pulsator*, is associated with ant nests. Females glow at dusk to attract mates. *Prolutacea* have been documented in Arizona, but otherwise very little is known about them.

Nelsonphotus

The genus *Nelsonphotus* is represented by a single species, *N. aridus*, found in Southern California. Courtship occurs at dusk (Buschman 2016). Very little is known about this glow-worm's life history or distribution.

Female glow-worms are flightless. Some unusual species, including those in the *Pleotomodes* and *Prolutacea* genera, are associated with ant nests. From top to bottom: *Microphotus angustus* (adult female), *Pleotomodes* sp. (adult male), *Prolutacea pulsator* (adult female), and *Nelsonphotus aridus* (adult male). (Photographs, from top: stevenw12339, Flickr CC BY-NC 2.0; Oliver Keller, iNaturalist CC BY-NC 4.0; Charles W. Melton; Joyce Gross.)

Daytime Dark Fireflies

As their name suggests, daytime dark fireflies are active during the day, and adults are not bioluminescent. Instead, communication is thought to occur using chemical pheromones. Similar to glow-worms, daytime dark fireflies are more commonly found in the West. Daytime fireflies are the least understood and studied of the three firefly groups found in the United States and Canada. Because species in this group are day active and generally do not flash or glow, it is possible that they have been overlooked.

Ellychnia

The *Ellychnia* are the most commonly encountered daytime dark fireflies in the United States and Canada, and they can be seen on colony trees in fall and winter. Adults become active in spring, when they can be found flying around or resting on vegetation. Sixteen species have been described from the United States and Canada. The most widespread and common species, *E. corrusca*, can be found from coast to coast and is often referred to as a species complex, likely representing several species, given the wide variety of habitats and morphological characters associated with this taxon.

Lucidota

This is another common genus, with three described species in the United States and Canada. Two *Lucidota* species, *L. atra* and *L. punctata*, fly throughout forests and forest margins in summer (Faust 2017). They can be found across much of the central and eastern United States and Canada. The third species, *L. luteicollis,* has flightless females (Lewis 2016a) and is found in Florida's dry scrub and sandhill habitats (Arnett et al. 2002). Hoping to shed some light on methods of communication in daytime dark fireflies, Lloyd (1972, cited in Lewis 2016a) conducted a simple yet classic study demonstrating that *L. atra* females attract mates by releasing pheromones. In the future, similar studies would no doubt provide much-needed information on the courtship behavior of our other daytime dark fireflies.

The two most commonly encountered daytime dark fireflies include species of *Ellychnia* (top) and *Lucidota* (bottom). (Photographs: Katja Schulz, Flickr CC BY 2.0.)

Pyropyga

Four species of *Pyropyga* are found from coast to coast in the United States and Canada, occupying a wide variety of habitats, from grassy fields and marshes to roadsides, ponds, and vegetable gardens. *Pyropyga* can often be found flying around flowers and other forbs in summer; two species have been documented nectaring on common milkweed (*Asclepias syriaca*) (Faust 2017).

Pterotus

While *Pterotus* is represented by two species of fireflies, only one (*P. obscuripennis*) is active during the day. The other, *P. curticornis*, is a night-time flyer (Pfeiffer 2019, pers. comm.) and appears restricted to southeastern California and Texas (Lyons 2018, pers. comm.; Pfeiffer 2019, pers. comm.). The Texas population, discovered in 2018, likely represents the easternmost known population, isolated to sky islands in protected canyons (Pfeiffer 2019, pers. comm.). The day-active species, *P. obscuripennis*, has flightless females and can be found in chaparral and foothills of the western United States and into Baja California, Mexico.

Brachylampis

The genus *Brachylampis* is known only from California, where two species have been described. Almost no information is available about these species.

Some daytime dark fireflies, such as *Pyropyga*, have been observed nectaring on flowers. From top to bottom: *Pyropyga* sp., *Pterotus obscuripennis*, and *Brachylampis* sp. (Photographs: top, Lynn Faust; center, Asa Spade, iNaturalist CC BY-NC 4.0; bottom, California Academy of Sciences, GBIF CC0 1.0.)

Pollaclasis

Another genus represented by a single species in the United States and Canada, *Pollaclasis* is uncommon but widespread (Faust 2017). Adults can be found in forests and small woodland openings throughout the eastern United States and into Ontario (Faust 2017). This is a poorly understood firefly with limited life-history information.

Paraphausis

The only described species within *Paraphausis*, *P. eximius*, occurs in Arizona. Its life history has not been described, except for the fact that females are flightless. *P. eximius* adults have no light organs and are therefore categorized as diurnal. However, it has been reported that males glow in the dark with their vestigial larval light organs (Stanger-Hall 2019, pers. comm.).

Tenaspis

Only one species of *Tenaspis* has been recorded in the United States—the tropic traveler (*T. angularis*). It appears to be very rare, observed only once or twice every ten years. Until recently, it was thought to be a tropical species found only in Florida and Texas, but it has now been tentatively reported from Missouri (Faust 2017, pers. comm.).

Relatively little is known about the fireflies in these three genera; it is possible that they are simply overlooked since they are active during the day, rather than at night like their flashing counterparts. From top: *Pollaclasis bifaria*, *Paraphausis* sp., and *Tenaspis angularis*. (Photographs: top, Giles Arbour, iNaturalist CC BY-NC 4.0; center, Joyce Gross; bottom, Eduardo Axel Recillas Bautista, iNaturalist CC BY-NC 4.0.)

Appendix B: Additional Resources

Field Guides

A growing number of illustrated field guides are available, making firefly education and identification more accessible to amateur enthusiasts and researchers alike. Here are a few key resources for learning more about fireflies and how to identify them.

Buschman, Larry. Unpublished manuscript, last modified March 2016. PDF. "Field Guide to Western North American Fireflies." https://entomology.k-state.edu/doc/WesternFireflies%20March%202016a.pdf. An online guide to fireflies found in the central and western United States, with a focus on species known from Kansas and Colorado.

Faust, Lynn. 2017. *Fireflies, Glow-worms, and Lightning Bugs*. Athens: University of Georgia Press. An identification guide for eastern and central North America, including flash patterns, activity periods, current research efforts, and natural-history notes.

Lewis, Sara. 2016. *Silent Sparks: The Wondrous World of Fireflies*. Princeton, NJ: Princeton University Press. An engaging introduction to the science and wonder of fireflies that explains the latest discoveries and descriptions of fireflies from around the world. Lewis explores current threats and ways to conserve firefly populations and includes a field guide to the most commonly encountered genera in North America.

Community Science Programs and Other Resources

Fireflyers International Network. https://fireflyersinternational.net. FIN is an international group of firefly scientists, conservationists, and artists. Their website provides a wealth of information on the global firefly community, upcoming meetings and symposia, and ways to get involved. An extensive list of published firefly literature is available, as well as numerous keys and field guides. In 2010 the group published the Selangor Declaration, which urges governments around the world to protect and restore firefly habitats, promote education and community involvement, and support funding for firefly-related research.

Mass Audubon, Firefly Watch. https://www.massaudubon.org/get-involved/citizen-science/firefly-watch. Mass Audubon has teamed with researchers from Tufts University to track firefly populations and determine if they are growing or shrinking and what could lead to changes in their populations. Participants commit to spending at least 10 minutes once a week during firefly season observing fireflies in one location in North America.

Natural History Museum of Utah, Western Firefly Project. https://nhmu.utah.edu/fireflies. The Natural History Museum of Utah is working with researchers at Brigham Young University to collect information on the firefly genus *Pyractomena* and investigate this group's phylogenetic relationships and population genetics. Community scientists can contribute to this effort by submitting observations of flashing fireflies from Utah and other western states.

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Personal Communications

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