

Notes

Chapter 1: Silent Sparks

A World of Wonder

To stay connected to wonder, I've drawn inspiration from the writings of Rachel Carson (Carson 1965) as well as from biologist Ursula Goodenough's compelling description of religious naturalism (Goodenough 1998).

More and more people are traveling to seek out fireflies in natural places. Information about firefly tourism comes from the following news stories. Estimates of tourist numbers in Taiwan, Thailand, and Malaysia come from e-mail correspondence with Dr. Tsung Hung Lee (Taipei; December 10, 2013), from Thancharoen (2012), and from Nada and colleagues (2009).

Chen, R. (2012, May 19). In search of Taipei's fireflies. *Taiwan Today*. Retrieved January 15, 2015, from <http://taiwantoday.tw>.

Brown, R. (2011, June 15). Fireflies, following their leader, become a tourist beacon. *New York Times*. Retrieved June 12, 2013, from http://www.nytimes.com/2011/06/16/us/16fireflies.html?_r=0

The unique significance of fireflies in Japanese art, literature, and culture is described by Yuma (1993), Ohba (2004), and Oba and colleagues (2011). For translating the first of these works, I am indebted to my colleague and friend, Ray Kameda.

Firefly Basics

The estimates about when in Earth's history both beetles and fireflies originated are taken from McKenna and Farrell (2009). They're based on so-called time trees, which are evolutionary trees whose time scales have been calibrated using dated fossils.

Patterns of firefly diversity and exotic species introductions are based on Lloyd (2002,

2008), and Viviani (2001). McDermott (1964) mentions the attempted introduction of *Photuris* fireflies into parks in Seattle and Portland. Majka and MacIvor (2009) describe how European glow-worms might have gotten accidentally introduced to Nova Scotia, and report on populations they found more than fifty years later in cemeteries around Halifax.

Looking for Love with Perfumes, Glows, and Flashes

Like all living creatures, fireflies carry their history in their genes. The evolutionary history of fireflies has been reconstructed by Branham and Wenzel (2001 and 2003) based on morphological traits, and by Stanger-Hall and colleagues (2007) based on DNA sequences.

Branham (2005) and Lewis (2009) give overviews about how different courtship styles in fireflies might have evolved.

Further Exploration

Silent Sparks: The TED Talk

https://www.ted.com/talks/sara_lewis_the_loves_and_lies_of_fireflies?language=en

If you're too busy to read this entire book then first watch my TED talk, which tells the condensed version of fireflies' story (14 minutes). Then come back here for a deeper dive!

Firefly Watch

<https://legacy.mos.org/fireflywatch/>

You can learn more about fireflies and sign up to report on your local lightningbug activity with this citizen science project hosted by Boston's Museum of Science.

The Fireflyer Companion

<http://entnemdept.ufl.edu/lloyd/firefly/>

Between 1993 and 1998, firefly expert Jim Lloyd distributed this informal newsletter dedicated to increasing awareness of firefly biology. Brimming with firefly facts, musings, poems, and even an occasional crossword puzzle, *The Fireflyer Companion* was a good vehicle for Lloyd's eclectic and sometimes rambling communication style. You can also download these from the *Silent Sparks* blog.

Chapter 2: Lifestyles of the Stars Deep in the Heart of the Smokies

Detailed descriptions of the life cycle, habits, and mating behavior of the Appalachian synchronous firefly *Photinus carolinus* appear in Faust (2010). Information about when, where, and how to see the Elkmont firefly display can be found on the National Park Service's website (<http://www.nps.gov/grsm/learn/nature/fireflies.htm>). *Photinus carolinus* is also found in Congaree National Park in South Carolina and in the Allegheny National Forest in Pennsylvania.

In his book *Sync: The Emerging Science of Spontaneous Order*, mathematician Steven Strogatz gives a highly entertaining and accessible description of the mathematical basis of synchronization and how it plays out in the engineered and natural world (Strogatz 2003).

Jon Copeland's quote is from:

Copeland, J. (1998). Synchrony in Elkmont: A story of discovery. *Tennessee Conservationist* (May–June).

The biographical material in this chapter is based on interviews I conducted with Lynn Faust in 2009, 2011, and 2013.

Humble Beginnings

Ferris Jabr lucidly describes how insects' complicated lifestyle might have evolved and gives some historical perspective about our scientific understanding of metamorphosis.

Jabr, F. (2012, August 10). How did insect metamorphosis evolve? Scientific American online. <http://www.scientificamerican.com/article/insect-metamorphosis-evolution>.

Many details of the larval habits of *Lampyris noctiluca* are based on John Tyler's informative pamphlet (Tyler 2002).

Their Glow Means No

Branham and Wenzel (2001) present phylogenetic evidence indicating that bioluminescence originated in the larval stage of some firefly progenitor, where it most likely functioned as a warning display.

Creative Improvisation: Fireflies Evolving

I've quoted Darwin's *The Origin of Species* (1859, p. 84) for what many consider his most poetic description of natural selection.

Synchronous Symphonies

Greenfield (2002) provides a cogent summary of various hypotheses for the evolution of synchrony in the courtship signals of various insects. Vencl and Carlson (1998) found that *Photinus pyralis* females preferentially respond to leading signals. Moiseff and Copeland (1995) looked at mechanisms of synchrony in *Photinus carolinus* fireflies, and Moiseff and Copeland (2010) showed that females responded more often to synchronous versus asynchronous male flashes.

Further Exploration

Darwin Online

<http://darwin-online.org.uk/>

Begun by Dr. John van Wyhe in 2002, this site provides digital, searchable versions of Charles Darwin's books, field notes, journals, and more, along with downloadable audio and image files.

Darwin in Print

Wilson, E. O., editor (2006). *From So Simple a Beginning: Darwin's Four Great Books*. W. W. Norton, New York, NY. 1706 pp.

Eminent biologist and Pulitzer Prize-winning author E. O. Wilson has annotated and gathered together four of Darwin's works in a beautifully illustrated and affordable volume: *Voyage of the H.M.S. Beagle* (1845), *The Origin of Species* (1859), *The Descent of Man and Selection in Relation to Sex* (1871), and *The Expression of Emotions in Man and Animals* (1872). In his afterword, Wilson thoughtfully examines divisions between science and religious belief.

The Life and Times of European Glow-Worms

The lifestyle of *Lampyris noctiluca* is showcased in vivid detail in two books by talented naturalists. The second is among the last works written by the great French entomologist J. Henri Fabre; though its literary style is rather florid for modern tastes, it remains entertaining.

John Tyler (2002). *The Glow-worm*. Privately published.

Fabre, J. H. (1924) *The Glow-worm and Other Beetles*. Dodd, Mead, New York, NY.

The UK Glow Worm Survey

<http://www.glowworms.org.uk/>

This informal group was set up Robin Scagell in 1990 to gather information about glow-worm sightings throughout the United Kingdom. The website describes the biology and conservation of

these glow-worms and provides links to many other resources and books.

Earth-Born Stars: Britain's Secret Glow-Worms

<https://vimeo.com/31952006>

This evocative short film by Christopher Gent shows larvae feeding on snails, illustrates female courtship habits, and explores conservation threats to one of Britain's most adored yet mysterious insects.

Chapter 3: Splendors in the Grass

Wild about Fireflies

Photinus fireflies were the main subject of Jim Lloyd's doctoral thesis (Lloyd 1966), where he described their geographic and habitat distributions, courtship behavior, and more. The frontispiece from this work is shown in [Figure 3.1](#) (used with permission from University of Michigan's Museum of Zoology), which artfully illustrates the male flight paths and flash patterns for the following *Photinus* species: (1) *consimilis* slow-pulse (2) *brimleyi*, (3) *consimilis* fast-pulse, (5) *marginellus*, (6) *consanguineus*, (7) *ignitus*, (8) *pyralis*, and (9) *granulatus*.

Defining the Indefinable

Charles Darwin's quote is from a letter written to his good friend and confidant, the botanist Joseph Hooker.

Darwin, C. R., Letter to J. D. Hooker. December 24, 1856. *Darwin Correspondence Database*.

<http://www.darwinproject.ac.uk/entry-2022>.

Heading Out into the Night

Carl Zimmer highlighted our firefly research in his award-winning article in the *New York Times*:

Zimmer, C. (2009, 29 June). Blink twice if you like me. *New York Times*. Retrieved from <http://www.nytimes.com/2009/06/30/science/30firefly.html>.

We describe the courtship behaviors of *Photinus greeni* fireflies in Demary and colleagues (2006) and Michaelidis and colleagues (2006).

A Light Snack

Lloyd (2000) reports tracking a couple hundred firefly males belonging to *Photinus collustrans* to see how likely they were to find a female versus encounter a predator. Various predators that feed on fireflies are described in Lloyd (1973a), Day (2011), and Lewis and colleagues (2012).

Closer Encounters

In Lewis and Wang (1991), we delve into the courtship and mating behavior of two New England fireflies, *Photinus marginellus* and *Photinus aquilonius*.

To the Victors Go the Spoils

Trivers (1972) suggested that differences in male and female sexual behavior resulted from the asymmetry in parental investment between the sexes. Biologist Darryl Gwynne and his colleague won an IgNobel Prize (“Achievements that make people laugh, and then think”) for discovering some males that aren’t choosy at all; in the Australian beetle *Julodimorpha bakervelli*, males often copulate with discarded beer bottles along the roadside (Gwynne and Rentz 1983).

Erica Deinert kindly showed me mate-guarding *Heliconius* butterflies in Costa Rica. Lynn Faust has described male pupal-guarding behavior in two fireflies, *Photinus carolinus* (Faust 2010), and *Pyractomena borealis* (Faust 2012).

Courtship is fiercely competitive for many *Photinus* fireflies, as described by Maurer (1968), Vencl and Carlson (1998), and Faust (2010). The hooked wing covers of male *Pteroptyx*

fireflies, which clamp around the female's abdomen during mating, were described by Wing and colleagues (1982). Lloyd (1979a) described the pseudo-female flash responses sometimes given by firefly males that have been unsuccessful in finding a female.

Ladies' Choice

The Darwin quote is from Part II, p. 38, of his book, *The Descent of Man and Selection in Relation to Sex* (1871), in which he describes what sexual selection is all about.

Fisher (1930) first modeled how female choice could trigger the elaboration of extravagant male bits such as the peacock's tail. Female choice in *Photinus* fireflies has been demonstrated using photic playback experiments conducted by Branham and Greenfield (1996), Cratsley and Lewis (2003), and Michaelidis and colleagues (2006). Demary and colleagues (2006) show that females preferentially give response flashes to certain males, and these males subsequently achieve higher mating success. Lewis and Cratsley (2008) provide a somewhat technical review of what scientists have learned about flash signal evolution, courtship, and predation in fireflies.

Trading Places

Lewis and Wang (1991) describe the seasonal shift in firefly sex ratios, and Cratsley and Lewis (2005) show that late-season males generally choose females who have more eggs.

Further Exploration

More on Sexual Selection

http://darwin-online.org.uk/converted/pdf/1871_Descent_F937.2.pdf

In the second part of his 1871 book, Darwin describes the power of sexual selection to shape

animal form and function. After outlining the principles and mechanisms of this fascinating evolutionary process, in separate chapters Darwin describes how sexual selection has led to the evolution of many wonderful and sometimes bizarre male features in crustaceans, mollusks, insects, amphibians, reptiles, birds, and even humans.

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. John Murray, London.

Here are two more excellent accounts of sexual selection—both shorter and also a bit wittier than Darwin's. Under the guise of a sex advice column for lovelorn beetles, stick insects, stalk-eyed flies, mice, and manatees, Olivia Judson's hilarious book describes some of the weird structures and behaviors that have evolved as a result of sexual selection.

Judson, O. (2002). *Dr. Tatiana's Sex Advice to All Creation*. Metropolitan Books, Henry Holt, New York, NY. 320 pp.

Cronin, H. (1993). *The Ant and the Peacock*. Cambridge University Press, New York, NY. 504 pp.

Traveling the Firefly Trail with Jim Lloyd

Jim Lloyd's monograph on US *Photinus* fireflies describes their geographic and habitat distributions, courtship flash behavior, and more, and is available free online:

Lloyd, J. E. (1966). Studies on the flash communication system in *Photinus* fireflies. *University of Michigan Miscellaneous Publications* 130: 1–95.

<http://deepblue.lib.umich.edu/handle/2027.42/56374>.

Between 1997 and 2003, Jim Lloyd published a series of articles in the open-access scientific journal *Florida Entomologist*, called “On Research and Entomological Education.”

Written in the form of letters addressed to his students, these ramblings are packed with information about firefly natural history, and are chock-full of ideas for field studies.

Lloyd, J. E. (1997). On research and entomological education, and a different light in the lives of fireflies (Coleoptera: Lampyridae; *Pyractomena*). *Florida Entomologist* 80: 120–31.

<http://journals.fcla.edu/flaent/article/view/74752>.

- Lloyd, J. E. (1998). On research and entomological education II: A conditional mating strategy and resource-sustained lek(?) in a classroom firefly (Coleoptera: Lampyridae; *Photinus*). *Florida Entomologist* 81: 261–72. <http://journals.fcla.edu/flaent/article/view/74829>.
- Lloyd, J. E. (1999). On research and entomological education III: Firefly brachyptery and wing “polymorphism” at Pitkin marsh and watery retreats near summer camps (Coleoptera: Lampyridae; *Pyropyga*). *Florida Entomologist* 82: 165–79. <http://journals.fcla.edu/flaent/article/view/74877>.
- Lloyd, J. E. (2000). On research and entomological education IV: Quantifying mate search in a perfect insect-seeking true facts and insight (Coleoptera: Lampyridae, *Photinus*). *Florida Entomologist* 83: 211–28. <http://journals.fcla.edu/flaent/article/view/59545>.
- Lloyd, J. E. (2001). On research and entomological education V: A species (c)oncept for fireflyers, at the bench and in old fields, and back to the Wisconsinian glacier. *Florida Entomologist* 84: 587–601. <http://journals.fcla.edu/flaent/article/view/75006>.
- Lloyd, J. E. (2003). On research and entomological education VI: Firefly species and lists, old and now. *Florida Entomologist* 6: 99–113. <http://journals.fcla.edu/flaent/article/view/75180>.

Chapter 4: With This Bling, I Thee Wed After the Lights Go Out

The demise of monogamy was reported by Natalie Angier in the *New York Times* in 1990. Some scientific ramifications of the “Polyandry Revolution” are explored in a theme issue introduced by Pizzari and Wedell (2013). We describe polyandry among *Photinus* fireflies in the wild in Lewis and Wang (1991).

Angier, N. (1990, August 21). Mating for life? It’s not for the birds or the bees. *New York Times*. <http://www.nytimes.com/1990/08/21/science/mating-for-life-it-s-not-for-the-birds-of-the-bees.html>.

Sperm Wars, Sperm Love

Leigh Simmons, an accomplished evolutionary biologist, provides a comprehensive review of

sperm competition theory and mechanisms in Simmons (2001). Quote about male genitalia and Swiss army knives is from p. 22 of Lloyd (1979b). Waage (1979) describes sperm removal in the damselfly *Calopteryx maculata*, and Davies (1983) reports cloacal pecking and sperm ejection by dunnocks, *Prunella modularis*.

Evidence for sexual selection via cryptic female choice is presented in two books, Eberhard (1996) and Peretti and Aisenberg (2015).

Amorous Bundles

We reported our discovery of nuptial gifts for *Photinus* fireflies in van der Reijden and colleagues (1997), and later for Japanese fireflies in South and colleagues (2008).

Finding the Perfect Gift

Different kinds of nuptial gifts, along with their evolutionary causes and consequences, are described in Lewis and South (2012) and Lewis and colleagues (2014). Albo and colleagues (2011) report that in the spider *Pisaura mirabilis*, males offering gift-wrapped worthless (inedible) gifts were as successful in obtaining mates as males that offered genuine gifts (dead flies). But females terminate matings sooner when males deceive them with worthless gifts, so these males have a disadvantage in sperm competition. Chemical ecologists Tom Eisner and Jerry Meinwald (1995) relate the astounding story of how ornate moths, *Utetheisa ornatrix*, sequester bitter-tasting alkaloids from their larval food plants, and how males then pass these toxins along to females in their nuptial gifts. Some intimate events that transpire during snail sex have been elucidated by Koene (2006).

Male Sexual Economics

We tested the notion that producing nuptial gifts is costly for male fireflies in Cratsley and colleagues (2003). In South and Lewis (2012), we found that males gain a paternity benefit from giving larger gifts because they get to sire a greater percentage of offspring.

Bright Lights and Bling: What's in It for the Female?

Demonstrating how valuable a nuptial gift can be when nutrients are scarce, Yoshizawa and colleagues (2014) describe cave-dwelling Brazilian bark lice whose female intromittent organ appears to have evolved through competition for male nuptial gifts.

As discussed in Lewis and colleagues (2004), gift giving plays an important role in firefly economics because most fireflies stop eating once they've become adults. In Rooney and Lewis (1999), we describe our radio-labeling studies showing that a female uses protein from the male's gift to help provision her eggs. In Rooney and Lewis (2002), we show that *Photinus ignitus* females who mate more often subsequently lay more eggs. In *Photinus greeni* females, a different benefit showed up: females who received larger gifts lived longer (South and Lewis 2012).

Cratsley and Lewis (2003) discovered a correlation between males' flash duration and their spermatophore size in *Photinus ignitus* fireflies; these females might be able to use a male's flash signals to predict what size gift he could offer. But when we looked for a similar relationship in *Photinus greeni* fireflies, we found none (Michaelidis et al. 2006).

Further Exploration

Animal Nuptial Gifts

In this short article we describe the astonishing diversity of nuptial gifts found across the animal kingdom:

Lewis, S. M., A. South, N. Al-Wathiqui, and R. Burns (2011). Quick guide: Nuptial gifts. *Current Biology* 21: 644–45.

<http://www.sciencedirect.com/science/article/pii/S096098221100604X>.

This excellent article published on Valentine’s Day by Brandon Keim in *Wired* online goes beyond the ordinary to illustrate animal nuptial gifts:

Keim, B. (2013, February 14). Freaky ways animals woo mates with gifts. *Wired*.

<http://www.wired.com/2013/02/valentines-day-animal-style/>.

From Dutch biologist and science writer Menno Schilthuizen come two informative books, both written with enthusiasm, clarity, and humor. *Nature’s Nether Regions* describes the reproductive equipment of barnacles, slugs, apes, and more, explaining how the bizarre and unusual inventions known as animal genitalia have been forged under postcopulatory sexual selection. His earlier book, *Frogs, Flies, and Dandelions* describes the history of ideas about how new species emerge, and explores the role that sexual selection might play in the speciation process.

Schilthuizen, M. (2014). *Nature’s Nether Regions*. Viking, New York, NY. 256 pp.

Schilthuizen, M. (2001). *Frogs, Flies, and Dandelions: Speciation—The Evolution of New Species*. Oxford University Press, Oxford. 256 pp.

Chapter 5: Dreams of Flying Into the Umwelt

The physiologist Jakob von Uexküll wrote a charming treatise exploring the sensory-perceptual worlds of different animals, as he explained and illustrated his concept of Umwelt (von Uexküll 1934). Healy and colleagues (2013) suggest that an organism’s perception of time depends on its size and metabolic rate, and find support for this idea using a phylogenetic comparison across different vertebrates.

Sexual Dimorphism

A deep exploration of anglerfish sex appears in an article by a world expert on such fish, Ted Pietsch (2005). South and colleagues (2011) report our discovery that in fireflies, females' flight ability is correlated with male nuptial gifts.

The King of Glow

The cultural association of Saint John's Eve with glow-worms is described in Raphaël De Cock's review of the biology and behavior of European fireflies (De Cock 2009). The biographical material in this chapter is based on interviews with Raphaël De Cock that I conducted in 2011 and 2013.

Raphaël De Cock's studies on luminescence acting as a warning signal for toads are reported in De Cock and Matthysen (2003). De Cock and Matthysen (2005) present evidence that females in the lesser European glow-worms use pheromones to attract mates.

Ghostly Glows and Phantom Fumes

Frick-Ruppert and Rosen (2008) describe blue ghost natural history and behavior. The fairies quote is taken from an entry on the blog called *Blue Ghost Post*, about Bennie Lee Sinclair and Don Lewis's Firefly Forest in South Carolina.

Blueghoster. *Saints, Sanctuaries, and The Blue Ghosts*. April 6, 2010.

<http://blueghostpost.blogspot.com/2010/04/saints-sanctuaries-and-blue-ghosts.html>.

The scientific report describing our blue ghost studies appears in De Cock and colleagues (2014). Dr. Somyot Silalom told me about the egg-guarding behavior of *Lamprigera tenebrosus* females. Studies on *Rhagophthalmus ohbai*, regarded as close kin to fireflies, reported that these bioluminescent, egg-guarding females release a volatile chemical that protects their eggs against

attack by soil microbes (Hosoe et al. 2014).

Further Exploration

The Glow-worm Song

<http://www.youtube.com/watch?v=2zOoAPn3OjQ>

Here you can enjoy “Glow Little Glow-Worm” as recorded by the Mills Brothers in 1952.

Sexual Dimorphism

This authoritative book by Daphne Fairbairn, an evolutionary biologist at the University of California, Riverside, explores the causes and consequences of the vast size differences between the sexes in particular species, including elephant seals, garden spiders, barnacles, and anglerfish.

Fairbairn, D. J. (2013). *Odd Couples: Extraordinary Differences between the Sexes in the Animal Kingdom*. Princeton University Press, Princeton, NJ. 312 pages.

Matt Simon describes anglerfish sexual habits in an article profusely illustrated with photographs (and a video) of dead fish.

Simon, M. (2013, November 8). Absurd creature of the week: the anglerfish and the absolute worst sex on Earth. *Wired*. <http://www.wired.com/2013/11/absurd-creature-of-the-week-anglerfish/>.

DuPont State Forest

The history of DuPont State Forest in North Carolina, located between Hendersonville and Brevard (<http://www.dupontforest.com/>) is described in this article. Formerly the site of a DuPont manufacturing facility, this state forest encompasses 4,200 hectares of preserved lands and is a good spot to see blue ghost fireflies during May.

Summerville, D. (2011). Southern Lights: Blue Ghost Fireflies. *Our State: North Carolina*.

<http://www.ourstate.com/lightning-bugs/>.

More on Blue Ghost Fireflies

These two reports describe what we currently know about blue ghost fireflies. Our 2014 article includes a supplementary video of blue ghost mating behavior

(<http://journals.fcla.edu/flaent/article/view/83837>).

Frick-Ruppert, J., and J. Rosen (2008). Morphology and behavior of *Phausis reticulata* (Blue Ghost Firefly). *Journal of North Carolina Academy of Science* 124: 139–47.

<http://dc.lib.unc.edu/cdm/ref/collection/jncas/id/3883>.

De Cock, R., L. Faust, and S. M. Lewis (2014). Courtship and mating in *Phausis reticulata* (Coleoptera: Lampyridae): Male flight behaviors, female glow displays, and male attraction to light traps. *Florida Entomologist* 97: 1290–307.

<http://dx.doi.org/10.1653/024.097.0404>.

Chapter 6: The Making of a Flasher

A Chemistry Set for Light

Reviews by Wilson and Hastings (1998, 2013) outline the chemistry of bioluminescence. The rendition of luciferase is from David S. Goodsell's June 2006 Molecule of the Month in the RCSB's Protein Data Bank (http://dx.doi.org/doi:10.2210/rcsb_pdb/mom_2006_6). Niwa and colleagues (2010) measured quantum yields of 40–60% from firefly bioluminescence.

Firefly Lights Evolving

Viviani (2002) and Oba (2015) review ideas about how beetle luciferases might have evolved.

Yuichi Oba and his colleagues (2008) measured luciferin content of various nonluminescent beetles. Lynch (2007) describes the role of gene duplication in the evolution of snake venom.

Darwin's prescient quote about exaptation is from the *Origin of Species* (1859, p. 190).

Putting Fireflies to Work

Practical applications for fireflies' light-producing ability are described in Weiss (1994), Rosellini (2012) and Andreu and colleagues (2013).

Weiss, R. (1994, August 29). Researchers gaze into the (insect) light and gain answers. *Washington Post*, A3.

Controlling the Flash

John Buck's biographical information is from Case and Hanson (2004), and from his *New York Times* obituary.

Pearce, J. (2005, April 3). John B. Buck, who studied fireflies' glow, is dead at 92. *New York Times*. <http://www.nytimes.com/2005/04/03/science/03buck.html>.

A Journey inside the Firefly Lantern

Buck (1948) and Ghiradella (1998) provide a detailed look at the internal anatomy of the firefly lantern. Not only an expert on firefly lantern anatomy, Helen Ghiradella is also a skilled artist whose drawings allow others to appreciate the internal architecture of this light-producing marvel. **Figure 6.2** is modified with permission from Ghiradella (1998).

Discovering the Firefly's Light Switch

Our discoveries about the role of nitric oxide in firefly flash control were reported in Trimmer et al. (2001). A complementary hypothesis about oxygen control based on the anatomy of firefly air tubes is presented by Ghiradella and Schmidt (2008).

Getting in Sync

Smith (1935) describes witnessing the synchronous fireflies (*Pteroptyx*) in Thailand, although he incorrectly concluded this activity was unrelated to mating.

John and Elisabeth Buck's trip to Thailand produced the very first scientific study of how *Pteroptyx malacca* fireflies manage to flash synchronously (Buck and Buck 1968). Elisabeth Buck's quote is from the Radiolab podcast, *Emergence*, broadcast on February 18, 2005. Bookending fifty years of scientific research on the mechanisms of firefly flash synchrony, John Buck wrote two review articles about the different physiological mechanisms underlying flash synchrony: Buck (1938) and Buck (1988). In the latter, he also describes the geographic and taxonomic distribution of several types of flash synchrony.

Science Confidential

Niko Tinbergen (1907–1988) was a Dutch ethologist and ornithologist who shared the 1973 Nobel Prize in Physiology or Medicine for his discoveries about animal behavior. His 1963 paper was dedicated to Konrad Lorenz on the occasion of the latter's sixtieth birthday. My account of this scientific feud is based on personal conversations and correspondence exchanged with both Jim Lloyd and John Buck. Buck and Buck (1978) focus their attention on how synchrony might benefit a group of males, while Lloyd (1973b) focuses attention on what advantages synchrony might provide to individual males as well as to the group. Faust (2010) describes how *Photinus carolinus* males switch from flashing synchronously to flashing chaotically as they approach a female. Case (1980) describes some close-up behavioral interactions inside *Pteroptyx* display trees.

Further Exploration

More about Bioluminescence

Living creatures that make their own light are deeply fascinating. The 2009 science fiction movie *Avatar*, written and directed by James Cameron, is well known for the exuberantly

bioluminescent creatures living on the fantasy world called Pandora. Two leading authorities on bioluminescence, Thérèse Wilson and Woody Hastings, describe the molecular details of bioluminescence in selected creatures, including fireflies.

Wilson, T., and J. W. Hastings (2013). *Bioluminescence: Living Lights, Lights for Living*. Harvard University Press, Cambridge, MA. 208 pp.

The *Bioluminescence Web Page* (<http://www.lifesci.ucsb.edu/~biolum/>) celebrates all living things that produce their own light (hosted by the University of California at Santa Barbara).

More about Synchrony

Writing for a general audience, leading mathematician and an award-winning science communicator Steve Strogatz explains how thousands of fireflies, cardiac pacemaker cells, or electrons in a superconductor manage to achieve their highly organized synchronous behavior without a conductor.

Strogatz, S. H. (2003). *Sync: The Emerging Science of Spontaneous Order*. Hyperion Books, New York, NY. 338 pp.

Biologist Michael Greenfield takes a detailed look at the acoustic, chemical, vibratory, visual, and bioluminescent signals that insects use to communicate with one another. He also reviews the hows and whys of collective male synchrony in fireflies, crickets, and cicadas.

Greenfield, M. (2002). *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Oxford University Press, New York, NY. 432 pp.

Radiolab: Emergence

<http://www.radiolab.org/story/91500-emergence/>

This February 18, 2005 Radiolab podcast explores how individuals following simple rules can generate complex group behaviors, like firefly synchrony. This episode features interviews with

biologists John and Elisabeth Buck, as well as with mathematician Steve Strogatz.

Chapter 7: Poisonous Attractions For the Love of Insects

Most of Tom Eisner's quotations were taken from video interviews he gave in 2000 for the *Web of Stories* project (see Further Explorations), or from this 2003 NPR interview. Others were from personal conversations I had with Tom during a visit to Cornell in 2008.

Eisner, T. (2003). Interviewed by Robert Siegel on *All Things Considered*, National Public Radio, November 18, 2003.

<http://www.npr.org/templates/story/story.php?storyId=1511501>.

Lightningbugs for Breakfast? No-No!

In addition to the *Web of Stories* video, Eisner relates a charming version of the Phogel story in his popular science book, *For Love of Insects* (Eisner 2003).

Jim Lloyd amassed more than a century's worth of anecdotal evidence about which creatures do and do not eat fireflies (Lloyd 1973). Knight and colleagues (1999) give detailed case histories about bearded dragons who met gruesome deaths by firefly. The bat study (Moosman et al. 2009) was conducted prior to the 2007 outbreak of white nose syndrome, a disease that has devastated bat populations in the eastern United States.

Chemical Weapons

The chemical defenses called lucibufagins were first identified by Tom Eisner and his colleagues (1978) from adults of three *Photinus* fireflies, which make these steroidal pyrones in several flavors. Lucibufagins have also been reported in adults of the diurnal firefly, *Lucidota atra* (Gronquist et al. 2006) as well as in larvae of *Lampyris noctiluca* (Tyler et al. 2008). Day (2011)

provides a review of firefly defenses.

Gao and colleagues (2011) provide an overview of the therapeutic potential of bufadienolide drugs, and Banuls et al. (2013) discuss the antitumor activity of thirty-five such compounds.

A Multifaceted Defense Strategy

Reflex bleeding was first described in *Photinus pyralis* by Blum and Sannasi (1974), and the phenomenon has since been reported from several other firefly genera, including *Pyrocoelia*, *Luciola*, and *Lucidina*. The pop-out defensive glands of firefly larvae were described for *Luciola leii* by Xinhua Fu and his colleagues (2007), and then again for several additional species in Fu et al. (2009). The dark side of the Smokies Light Show is explored in Lewis et al. (2012).

Evolution of Warning Displays

The many years that Alfred Russel Wallace spent doing fieldwork in the tropics helped him grasp the concept of warning coloration more readily than did Darwin. He described cryptic coloration, warning displays, and mimicry in his 1867 article (quote appears on p. 9). Wallace used the term “danger-flag” in his 1889 book on natural selection (p. 232). The Darwin quote is from a letter written at Down House to A. R. Wallace dated February 26, 1867 (F. Darwin 1887, p. 94)

De Cock and Matthysen (2001) showed that firefly color patterns act as a warning signal for starlings. Other studies have demonstrated the power of glows to facilitate avoidance learning in toads (De Cock and Matthysen 2003), mice (Underwood et al. 1997), spiders (Long et al. 2012), and bats (Moosman et al. 2009).

Firefly Look-Alikes: Tasty or Toxic?

Bates wrote extensively about his travels and natural history observations (see Further Explorations). Quotation is from his 1862 paper on mimicry among Amazonian butterflies (Bates 1862, 507).

The photographs of firefly mimics in [Figure 7.3](#) are (clockwise from upper left): a cockroach (Blattellinae), *Pseudomops septentrionalis* (photo by John Hartgerink); a blister beetle (Meloidae), *Pseudozonitis* sp. (photo by Mike Quinn, TexasEnto.net); a longhorn beetle (Cerambycidae), *Hemierana marginata* (photo by Patrick Coin), a net-winged beetle (Lycidae), *Plateros* sp. (photo by Gayle and Jeanell Stickland), a moth (photo by Shirley Sekarajasingham), and a soldier beetle (Cantharidae), *Rhagonycha lineola* (photo by Patrick Coin).

The Vampire Firefly

Aggressive mimicry by *Photuris* femmes fatales was described by Lloyd (1965, 1975, 1984).

Tom Eisner and his colleagues (1997) showed that *Photuris* females sequester their prey's toxic lucibufagins, stockpiling them for their own self-protection. While femmes fatales acquire the vast majority of their lucibufagin from prey, these researchers also found tiny amounts of lucibufagin in some lab-reared *Photuris* that never had access to *Photinus* prey. Andres González and his colleagues (1999) noted that *Photuris* larvae have an endogenous defensive chemical, known as betaine, which carries over into adults and affords them some limited protection against predators. They also showed that females endow their eggs with high concentrations of the lucibufagins that they have sequestered from their prey.

Lloyd and Wing (1983) and Woods and colleagues (2007) describe hawking by *Photuris* predators, and Faust and colleagues (2012) describe the kleptoparasitic behavior of these thieves in the night.

Further Exploration

More about Tom Eisner

Web of Stories

<http://www.webofstories.com/play/thomas.eisner/7>

This online repository contains video interviews with some of the greatest scientists of our time.

Tom Eisner is one, and he talks about his life and work in several segments. In *Why Entomologists Eat Bugs: A Firefly Story*, Eisner tells how he and Phogel discovered the chemicals that help fireflies defend themselves against predators.

A gifted communicator, Eisner's 2003 book provides an entertaining account of his many explorations in the land of chemical ecology, vividly illustrated with his own spectacular photographs.

Eisner, T. (2003). *For Love of Insects*. Belknap Press of Harvard University Press, Cambridge, MA. 464 pp.

Light Snacks: Predation on Fireflies

<http://vimeo.com/28816083>

This short video by the Lewis Lab shows field observations of fireflies under attack by spiders, bugs, and the predatory *Photuris* femmes fatales, based on research by Sara Lewis, Lynn Faust, and Raphaël De Cock. The Griff Sextet provided the soundtrack, which features scientist and musician Raphaël De Cock on vocals.

More about Warnings and Mimicry

Ruxton and colleagues provide an outstanding and readable explanation, though perhaps a bit technical, of what's known concerning the evolution of cryptic coloration, warning signals, and mimicry in animals.

Ruxton, G. D., T. N. Sherratt, and M. P. Speed (2004). *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry*. Oxford University Press, Oxford.

Quite popular when first published in 1863, this nineteenth-century classic chronicles travels through the Amazon basin by Henry William Bates, the British naturalist and insect collector. His wide-ranging and charming account covers natural history, geography, ethnography, and more. One admirer, Charles Darwin, called it “the best work of natural history travels ever published in England.” A hundred fifty years down the road, it remains an enviable model of lyrical nature writing.

Bates, H. W. (2009). *The Naturalist on the River Amazon*. Cambridge University Press, Cambridge, UK.

Chapter 8: Lights Out for Fireflies? Darkening Summers

Keneagy (1993) reported on dwindling numbers of fireflies in Florida. The firefly e-mails appeared on a website maintained by Donald Ray Burger, a personal injury lawyer and firefly fan based in Houston, Texas. This site (<http://www.burger.com/firefly.htm>) provides links to lots of useful firefly information; since 1996 Burger has been collecting and posting hundreds of reports he receives about firefly numbers from all over North America.

Keneagy, B. (1993, September 25). Lights out for firefly population. *Orlando Sentinel*.

http://articles.orlandosentinel.com/1993-09-25/news/9309250716_1_lightning-bugs-fireflies-osceola.

Estimates of firefly declines in Thailand are from Casey (2008) and New Tang Dynasty TV’s news story about declining firefly populations along the Mae Klong River in Bam Lomtuan, southern Thailand.

Casey, M. (2008, August 30) Lights out? Experts fear fireflies are dwindling. *USA Today*.

http://usatoday30.usatoday.com/news/world/2008-08-30-1331112362_x.htm.

New Tang Dynasty Television (2009, June 10). *Fireflies' spectacle coming to an end*. (Video file). <http://www.youtube.com/watch?v=06RHUmVQ-e8>.

Paved Paradise

Jim Lloyd's quote about the absence of fireflies in Houston appeared in a news story by Grossman (2000).

Grossman, W. (2000, March 2). Fireflies are disappearing from the night sky. *Houston Press*. Retrieved from <http://www.houstonpress.com/issues/2000-03-02/feature2.html>.

Jusoh and Hashim (2012) describe how the loss of mangrove habitat has affected the Malaysian synchronous firefly, *Pteroptyx tener*, and Thancharoen (2012) discusses firefly tourism and conservation in Thailand.

Sonny Wong provides advice about good firefly-watching behavior on his blog about Malaysian fireflies: <https://malaysianfireflies.wordpress.com/2010/01/20/firefly-watching-ethics/>. His quote is from an interview with Sharmilla Ganesan (2010).

Ganesan, S. (2010, February 16). Keeping the lights on. *The Star Online*. <http://www.thestar.com.my/Lifestyle/Features/2010/02/16/Keeping-the-lights-on/>.

Drowning in Light

David Owen (2007) wrote about the International Dark-Sky Association.

Owen, D. (2007, August 20). The dark side: Making war on light pollution. *New Yorker*. <http://www.newyorker.com/magazine/2007/08/20/the-dark-side-2>.

Ineichen and Rüttimann (2012) describe how artificial light affects European glow-worms. Rich and Longcore (2006) explore the ecological consequences of artificial illumination, including effects on nest choice and breeding success of birds to behavioral and physiological changes in salamanders. One chapter by Jim Lloyd speculates about how stray light could affect fireflies.

A Bounty on Firefly Lights

Pieribone and Gruber (2005, p. 101) reproduced a photo taken at Johns Hopkins “before the molecular biology revolution” with William McElroy sitting next to an enormous pile of bounty-hunted fireflies, preparing to extract their luciferase. I’ve met some people who collected for McElroy when they were kids, and they still recall the excitement of running around Baltimore at night, gathering fireflies to trade in for cash the next day.

The *Chicago Tribune* reported on the Sigma Chemical Company’s firefly-collecting activities in 1987, as did Valerie Reitman in the *Wall Street Journal* in 1993. Searching for “Firefly Scientist’s Club” in Google News will turn up many old newspaper advertisements soliciting collectors to help in harvesting fireflies for commercial sale.

United Press International (1987, August 24). Pennies from heaven for firefly catchers. *Chicago Tribune*. http://articles.chicagotribune.com/1987-08-24/business/8703040337_1_fireflies-sclerosis-and-heart-disease-shark-tank.

Reitman, V. (1993, September 2) Scientists are abuzz over the decline of the gentle firefly. *Wall Street Journal*. A1.

As of 2015, many firefly-derived products are still listed on the Sigma-Aldrich website, including:

Dried firefly tails (abdomens) <http://www.sigmaaldrich.com/catalog/product/sigma/fft>.

Whole dried fireflies <http://www.sigmaaldrich.com/catalog/product/sigma/ffw>.

Gilbert (2003) describes firefly-collecting efforts in Morgan County, Tennessee, led by Pastor Dwight Sullivan from Whittier, California. As reported by O’Daniel (2014), during the summer of 2014 Sullivan was paying \$2 per 100 live fireflies collected. In Bauer et al. (2013), we developed a model to predict whether firefly populations could sustain various levels of harvesting.

Gilbert, K. (2003, June 20). Fireflies light the way for this pastor. *United Methodist Church*

News. http://archives.umc.org/umns/news_archive2003.asp?ptid=&story={661B5CCE-59B8-4C1F-8BF3-F0F17B99DDE6}&mid=2406.

O'Daniel, R. (2014, July 16). Blicking bucks: Scientists will pay for summer's glow. *Morgan County News*. <http://www.morgancountynews.net/content/blinkin-bucks-scientists-will-pay-summer-glow>.

Other Insults

Estimates of pesticide application rates are from Beyond Pesticide's website, which provides fact sheets, news, and advocacy around the human health and environmental effects of pesticides:

Beyond Pesticides Fact Sheet (August 2005). *Lawn Pesticides Facts and Figures*.

http://beyondpesticides.org/lawn/factsheets/LAWNFACTS&FIGURES_8_05.pdf.

Ki-Yeol Lee and colleagues (2008) provide a comprehensive study that experimentally measured how pesticides and fertilizers affect the different life stages of the common Asian firefly, *Luciola lateralis* (now renamed *Aquatica lateralis*); this firefly spends its larval stage living underwater. Analyzing the time course of firefly declines, Masahide Yuma (1993) pointed to increasing pesticide use on rice fields as a factor contributing to declining populations of Japanese fireflies. I am indebted to my former student and now colleague Ray Kameda for translating this and other material from Japanese.

Hotaru Koi: Come Firefly!

Erik Laurent (2001) and Akito Kawahara (2007) provide excellent descriptions of Japanese entomophilia. The deep appreciation felt for fireflies in Japanese culture is described by Yuma (1993), Ohba (2004), and Oba and colleagues (2011).

Lafcadio Hearn (1850–1904) was a popular writer, translator, and interpreter of Japanese life and culture. The quotes are from his 1902 piece “Fireflies” reprinted on pp. 188–94 in Allen and Wilson's 1992 anthology of Hearn's writings.

Yuma (1995) traces the history of Uji's fireflies. The late-night oviposition behavior of Genji-botaru females was described by Yuma and Hori (1981). The Tokyo Hotaru Festival (<http://tokyo-hotaru.jp/>) is now held annually in May.

Spacey, J. (2012, June 14). Hotaru Festival: A light spectacular in Tokyo. *Japan Talk*.
<http://www.japan-talk.com/jt/new/tokyo-hotaru-festival>.

Iguchi (2009) reports evidence that local fireflies in the town of Tatsuno, Nagano Prefecture, which holds an annual summer firefly festival, have been contaminated by releasing nonnative, artificially bred Genji fireflies from other regions.

Further Exploration About Fireflies in Japan

Beetle Queen Conquers Tokyo is a fascinating 2009 documentary produced and directed by Jessica Oreck, which takes a closer look at the Japanese enthusiasm for insects, especially beetles.

The Tokyo Hotaru Festival is featured in this short video (<https://vimeo.com/67980309>), which shows artificial fireflies being launched onto the Sumida River as it flows through downtown.

Selangor Declaration on the Conservation of Fireflies

<http://www.lampyridjournal.com/the-selangor-declaration-conservation-of-fireflies/>

Written by an international group of firefly experts in 2010 in Selangor, Malaysia, this declaration was updated in 2014.

The International Dark-Sky Association

<http://www.darksky.org/>

This nonprofit group works to spread the word about light pollution and provides resources to help preserve the night.

Field Guide Notes

E. O. Wilson's quote is from p. 139 of Wilson (1984). I'm grateful to the photographers who generously provided their wonderful firefly portraits for this field guide: *Photinus*, *Photuris*, and *Ellychnia* photos are by Croar.net, *Pyractomena angulata* photo is by Stephen Cresswell, *Pyractomena borealis* photo is by Richard Migneault, and *Lucidota atra* photo is by Patrick Coin.

For distinguishing fireflies from other similar-looking beetles, there are several excellent beetle identification guides, including:

White, R. E. (1998). *A Field Guide to the Beetles of North America*. Houghton Mifflin Harcourt, New York, NY.

BugGuide (<http://bugguide.net>) is a free online resource hosted by Iowa State University. A dedicated team of entomologists provides identifications for insect photos uploaded by curious naturalists from all over the United States and Canada.

Evans, A. V. (2014). *Beetles of Eastern North America*. Princeton University Press, Princeton, NJ.

Firefly Guides around the World

Field guides to the local firefly fauna have been published for many regions, including Taiwan, Hong Kong, Portugal, China, and Japan. John Day's informative website *Fireflies and Glow-worms* (<http://www.firefliesandglow-worms.co.uk/key-to-firefly-genera.html>) includes a key to European genera.

Chen T. R. (2003). *The Fireflies of Taiwan*. Field Image Press, Taipei City, Taiwan. 255 pp. (in Chinese).

De Cock, R., H. N. Alves, N. G. Oliveira, and J. Gomes (2015). *Fireflies and Glow-Worms of Portugal (Pirilampos de Portugal)*. Parque Biológico de Gaia, Avintes, Portugal. 80 pp. (in Portuguese and English).

Fu, X. (2014). *Ecological Atlas of Chinese Fireflies*. Commercial Press, Beijing. 167 pp. (in Chinese).

Ohba, N. (2004). *Mysteries of Fireflies (Hotaru Tenmetsu no Fushigi)*. Yokosuka City Museum, Yokosuka, Japan (in Japanese).

Vor, Y. (2012). *Fireflies of Hong Kong*. Hong Kong Entomological Society, Hong Kong. 117 pp. (in Chinese).

Surprisingly, until now there haven't been any comprehensive field guides to North American fireflies, though the following resources are quite useful:

Firefly Watch (<https://legacy.mos.org/fireflywatch>). Hosted by the Boston Museum of Science, this site provides descriptions and flash charts for *Photinus*, *Pyractomena*, and *Photuris* lightningbugs.

Faust, L. (2017). *Fireflies, Glow-Worms, and Lightning Bugs! Natural History and a Guide to the Fireflies of the Eastern US and Canada*. University of Georgia Press, Athens.

Lloyd, J. E. (1966). Studies on the flash communication systems of *Photinus* fireflies. *University of Michigan Miscellaneous Publications* No. 130.

<http://deepblue.lib.umich.edu/handle/2027.42/56374>.

Luk, S.P.L., S. A. Marshall, and M. A. Branham (2011). The fireflies (Coleoptera: Lampyridae) of Ontario. *Canadian Journal of Arthropod Identification* 16.

http://www.biology.ualberta.ca/bsc/ejournal/lmb_16/lmb_16.html.

Majka, C. G. (2012). The Lampyridae (Coleoptera) of Atlantic Canada. *Journal of the Acadian Entomological Society* 8: 11–29. <http://www.acadianes.org/journal.php>.