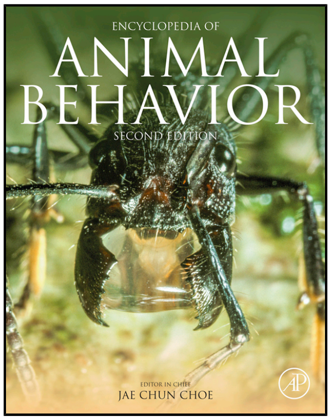

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Bioluminescent Signals

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Mysterious glows or flashes have fascinated human observers for over 3000 years and appear in the folklore of Europe, Asia, Africa, and the Americas, with the firefly as one of the most common insects in Mayan art (Roda, 2011). Whether in the depth of the ocean, in crashing waves at the beach, or as aerial light displays during mid-summer nights, what we are witnessing is nothing less than a quest for survival and reproduction by an astonishing diversity of organisms. Bioluminescence, the conversion of chemical energy into light by living organisms, is a widespread phenomenon across the tree of life. It may have evolved at least 40 times in a wide range of taxonomic groups, including bacteria, dinoflagellates, fungi, jellyfish, squid, crustaceans, snails, annelids, insects, and vertebrates (Haddock *et al.*, 2010), with more than seven unique biochemical systems (Hastings, 1983; Petushkov and Rodionova, 2005; Viviani *et al.*, 2002; Fallon *et al.*, 2018) adopted for light production. In this article we introduce the diversity of bioluminescent signals in the context of animal communication, with a focus on the structure, function and evolution of bioluminescent signaling behavior.

Bioluminescence

The Chemical Diversity of Bioluminescence

Bioluminescence is generated by oxidation reactions, but the specific chemistry varies greatly among organisms (Hastings, 1983). Bioluminescence requires two principal components: a light emitter that is oxidized (generically called luciferins, although specific structures vary) and a catalyzing enzyme (generically called luciferases, although not members of one protein family). Some marine organisms use photoproteins, associated with specific triggers, instead, e.g., the photoproteins of cnidarians, ctenophores, and radiolarians require Ca^{2+} to trigger their luminescence (Shimomura, 1985). Luciferins are conserved across some light-emitting organisms. For example, all beetles share an identical beetle luciferin (Day *et al.*, 2004), while another luciferin, coelenterazine, is the light emitter for nine different marine phyla (Haddock *et al.*, 2010). Depending on the group, luciferins can be dietary, or are biochemically produced (Haddock *et al.*, 2001). In contrast, luciferases are considerably more diverse and species–specific. Their high sequence variability is associated with differences in light emission colors among beetles (Viviani, 2002). The molecular biology of different luciferases, and especially the amino acids causing shifts in light-color of firefly luciferases, are exceptionally well characterized due to their importance in biotechnology and biomedical reporter systems (e.g., Fraga, 2008; Welsh and Kay, 2005).

Intrinsic Versus Symbiotic Bioluminescence

Many bioluminescent organisms have evolved their own intrinsic bioluminescent chemistry, while others derive their bioluminescence from symbiotic relationships with bioluminescent bacteria (Haddock *et al.*, 2010), which requires the evolution of specialized structures to permanently house the bacteria and intricate interactions between hosts and symbionts (e.g., McFall-Ngai, 2014, for potential bacterial benefits see Stabb, 2005). Symbiotic relationships with bioluminescent bacteria contribute greatly to the diversity of bioluminescent signaling in the ocean. For example, a recent study determined that bioluminescence in 1500 species of fish evolved independently at least 27 times (Davis *et al.*, 2016). In 17 of these instances bioluminescent bacteria were taken up as symbionts to generate bioluminescence. There is a remarkable diversity of bioluminescent chemistry within genera and within species (Widder, 2010; Takenaka *et al.*, 2012). Even more intriguing, there can be multiple chemistries within individuals. For example, adult females of the deep-sea anglerfish *Linophryne coronata* have two different light-emitting systems: bacterial luminescence in the dorsal lure, and an intrinsic, unidentified chemistry in the chin barbel (Widder, 2010).

Bioluminescent Body Parts Versus Secretions

Adding yet another layer of complexity to the study of bioluminescent signals, luminescent reactions can take place in secretions outside the body, or in specialized cells (photocytes) or "light organs" (photophores) of varying morphological complexity, including some with added light reflectors and lenses to focus the direction of bioluminescence (Herring, 2000). In some instances (e.g., bobtail squid), the light production of bacterial symbionts is monitored by a visual pigment in the light organ, which functions as an "inner eye" that can produce bioluminescence as well as perceive it, and could enable the host to impose selection for bioluminescence on its symbiotic bacteria (McFall-Ngai, 2014). Interestingly, visual pigments are also expressed in the light organs of some fireflies (Fallon *et al.*, 2018) with unknown function. Organisms that generate bioluminescence with both, light organs as well as bioluminescent secretions, include the shrimp *Systellaspis* and *Oplophorus* (Herring, 1983; Latz *et al.*, 1988), and the deep-sea vampire squid *Vampyroteuthis*, which release glowing particles into the water, apparently to distract predators (Haddock *et al.*, 2010).

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Why Use Bioluminescence?

Bioluminescence is a very effective way to communicate in dark environments as long as the visual pathway is unobstructed (Haddock *et al.*, 2010). Depending on the environmental conditions, a bioluminescent flash can be seen from tens to hundreds of meters away in the ocean (Warrant and Locket, 2004), as well as on land (KSH personal observation). The vast majority of bioluminescent organisms are found in marine environments (**Fig. 1**). The abundance of marine bioluminescence may be partly due to the older age of the lineages living in this environment, partly due to widespread bioluminescent symbionts, and/or to the expanse of the oceans, with light penetrating only the surface layers, leaving most of the ocean environment in perpetual darkness. Yet even shallow ocean waters, dark only at night, harbor luminous organisms. In an extensive study off the California coast, 76% of all individual animals (in 553 taxa) observed between the surface and a depth of 3900 m are known to be luminous, with little variation with depth (Martini and Haddock, 2017). In contrast, only about 25% of 746 bioluminescent genera analyzed to date are found in terrestrial environments, with bioluminescent beetles contributing most genera (Oba and Schultz, 2014). For extensive surveys of known bioluminescence see the excellent reviews by Lloyd (1983), Viviani (2002), Oba and Schultz (2014), Herring (2007), Haddock *et al.* (2010), Widder (2010), Verdes and Gruber (2017), among others.

Bioluminescent Signals

Communication signals and crypsis (obscurement of potential cues for unintended receivers) mediate key interactions between organisms in ecological communities. In the communication framework a light signal has to elicit an observable change in the behavior of the intended receiver to be considered a signal. This definition separates bioluminescent communication signals from the use of bioluminescence for crypsis (elimination of body shape cues by counterillumination: Young and Roper, 1976), however many marine animals use their bioluminescence for both. For example, the firefly squid (*Watasenia scintillans*) ascends from the deep ocean at night to form large near-surface aggregations during the spawning season; it uses its ability to sense and to produce light for counter-illumination, making it difficult for predators to detect it from below, however at the surface it may light up its whole body to attract a mate (Barratt and Allcock, 2014). Just like any other communication signals, bioluminescent signals are shaped by natural and/or sexual selection in the specific context and environment they are used, ultimately impacting both the signaler's and the receiver's fitness (Endler, 1992, 1993). Other definitions of animal communication signals require mutual benefits to signalers and receivers (Alcock, 2010), essentially limiting communication to honest signaling. However, we use a somewhat wider definition here, including signals to manipulate the behavior of potential prey and potential predators to the main benefit of the signaler and at a cost to the intended receiver.

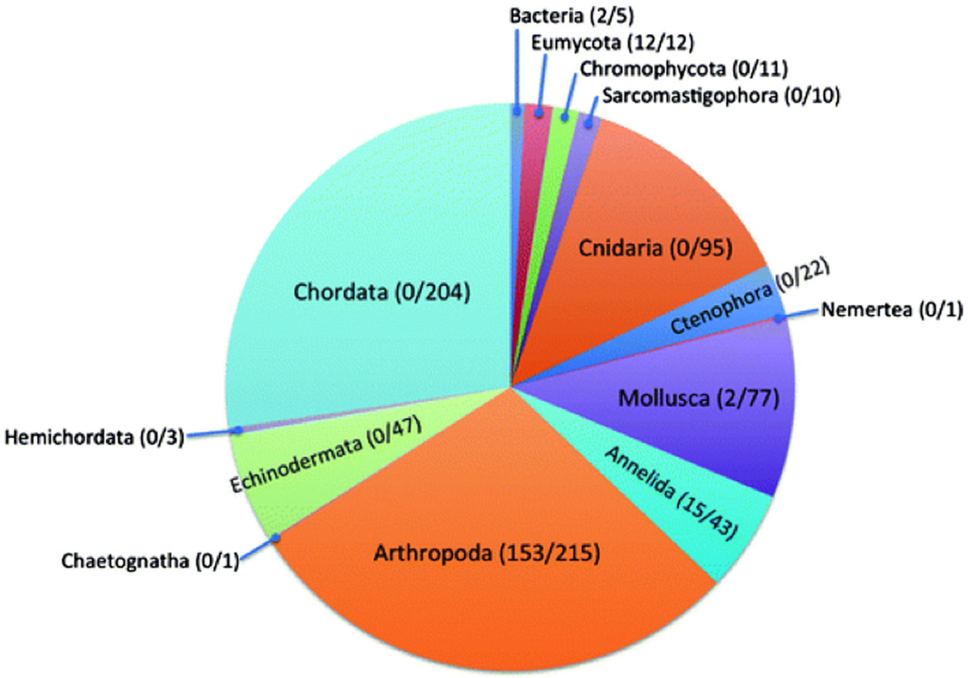


Fig. 1 The diversity of bioluminescent organisms as proportion of 746 genera analyzed. With permission from Oba, Y., Schultz, D.T., 2014. Eco-evo bioluminescence on land and in the sea. In: Bioluminescence: Fundamentals and Applications in Biotechnology, vol. 1. Berlin, Heidelberg: Springer, pp. 3–36.

For successful communication a signal has to be generated, travel through the environment and be detected and processed by the intended receiver before the receiver can respond.

Signal Production

Signal phenotypes

Bioluminescent signals can be short (flashes) or long (glows), however, these are somewhat subjective distinctions along a temporal continuum; sometimes longer signals are labelled as flashes due to their initially high, but declining brightness. Ideally, when describing signal phenotypes, these description would be accompanied by time measurements, however this is not always possible, especially for marine animals. Therefore we propose the following working definition here: a "flash" is a short light emission (<2 seconds) with a rapid increase and decrease in intensity (see also Morin, 1983), and a "glow" is a sustained (>2 s) signal that may vary greatly in duration. For example, the single flashes of North American fireflies (Stanger-Hall and Lloyd, 2015), ostracods in the genus *Photeros* (Morin and Cohen, 2010), and lanternfishes (Mensinger and Case, 1997) last less than 1 s. Glows are emitted by the larvae of all firefly species, by larviform firefly females and by a few firefly males (DeCock *et al.*, 2014), as well as the larvae and adults of other bioluminescent beetles (Viviani and Santos, 2012). In ostracods glows often last up to 15 s (Morin and Cohen, 2010). In addition to these descriptions of light emission phenotypes, "pulses" are used to describe individual signal components within complex flash patterns (**Fig. 2**), much like "pulses" are used as components of complex calls in the acoustic literature (Gerhardt, 1992). In the ocean, "pulses" describe combinations of individual flashes and/or glows generated by a series of bioluminescent secretions in ostracod courtship displays (Morin and Cohen, 2010).

Biochemistry of signal phenotypes

All light signal phenotypes are a direct result of the underlying bioluminescence chemistry, specifically the rates of enzyme turnover and substrate availability. While in many bioluminescent taxa this chemistry is hidden within photocytes and/or light organs, it is exposed in the bioluminescent secretions of marine ostracods, providing a rich study opportunity for the quantification of bioluminescent signal traits.

Although differences in direction and distance between the pulsed secretions of ostracods are determined by male swimming behavior, other aspects of courtship displays are dominated by the biochemistry of the luciferin:luciferase reaction, which occurs in secreted mucus outside the body and therefore is not under direct behavioral control. In particular, biochemistry determines the brightness, duration, and decay rate of individual pulses (**Fig. 3**).

Signal context

Bioluminescent signals are visual signals that are produced for specific intended receivers in three main contexts: (1) Predator defense: startle predators, illuminate predators and increase their predation risk, or as an aposematic signal to warn predators of unprofitability; (2) Food acquisition: locate food by means of built-in headlights or attract prey with light or glowing lures, exploiting their phototropic behavior; (3) Reproduction: locate and/or attract mates with species-specific temporal and spatial patterns of light emissions. Despite these clear categories, many organisms use variants of their bioluminescent signals in more than one context. For example, some fish can control their light with the help of their nervous system, using it not just to lure prey, but also potentially for intra-specific communication (Haddock *et al.*, 2010; **Fig. 4(A)**), and most luminous insects use their light signals for courtship, as well as anti-predator defense or prey attraction (Lloyd, 1983; **Fig. 4(B)**).

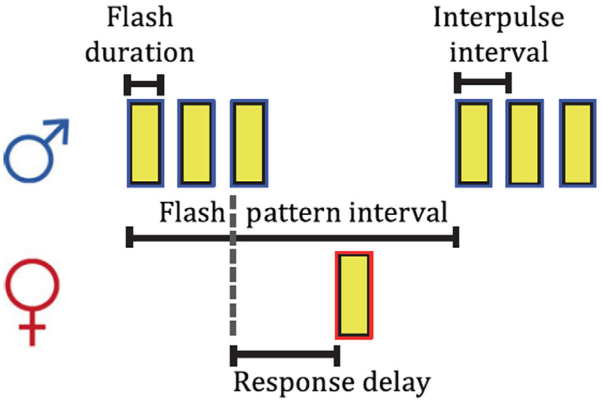


Fig. 2 Flash signal traits of fireflies. Shown is a 3-flash flash pattern that is repeated at regular flash pattern intervals. Inter-pulse intervals describe the temporal spacing of flashes within multi-flash flash patterns. From Stanger-Hall, K.F., Lloyd, J.E., 2015. Flash signal evolution in *Photinus* fireflies: Character displacement and signal exploitation in a visual communication system. Evolution 69(3), 666–682.

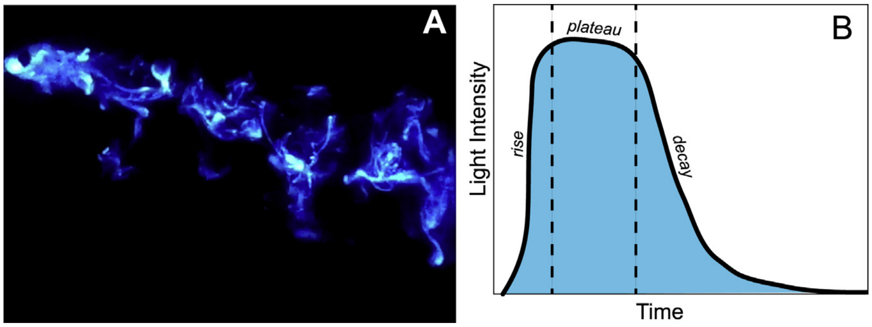


Fig. 3 (A): A cardinalfish (Apogonidae) is illuminated by the anti-predator response of a cypridinid ostracod. The cypridinid released a large cloud of bioluminescent mucus and swam away safely after a predation attempt in a staged aquarium setting. (Photo captured from video by N. Hensley and T. Rivers). (B): Light pulses are created as large anti-predator displays and also as small light pulses that form components of courtship displays. The duration of light pulses in secreted luminescence is determined by three phases: rise, plateau, and decay. In the rise phase the substrate and enzyme are first secreted and light intensity increases over time. During the plateau phase, the enzyme is limiting and total pulse duration will be determined by the enzyme:substrate ratio. In the decay phase, the substrate is limiting, resulting in an exponential decay of light as the substrate is used up. From Hensley, N.M., Ellis, E.A., Gerrish, G.A., *et al.*, 2018. Phenotypic evolution shaped by current enzyme function in the bioluminescent courtship signals of sea fireflies. (Submitted).

(1) *Predator defense (intended receivers: potential predators)*. Phylogenetic and ontogenetic evidence suggests that bioluminescent signaling likely originated as anti-predatory response, often in immature life-stages, of many bioluminescent animal lineages, while bioluminescent signaling in adults is derived. For example in bioluminescent cypridinid ostracods worldwide, all instars of either sex produce antipredatory bursts of light when disturbed (Morin and Cohen, 2010), but only male cypridinid ostracods from reefs in the Caribbean Sea, phylogenetically nested within the broader luminous group, produce bioluminescent courtship displays (Morin, 1986; Cohen and Morin, 2003). Similarly, all known firefly (Lampyridae) larvae of 2000+ species worldwide emit green larval glows as aposematic warning signals, directed at potential predators (Sivinski, 1981; Underwood *et al.*, 1997; DeCock, 2009), while the adults of many, but not all, firefly species generate glows or flashes as anti-predator and courtship signals (Lloyd, 1971). Honest aposematic defense glows advertise powerful toxins, e.g., the lucibufagins (cardiotoxic steroids) of *Photinus*, *Ellychnia* and *Lucidota* fireflies (Eisner *et al.*, 1978; Smedley *et al.*, 2017) or the cyanide of bioluminescent *Motyxia* millipedes (Marek *et al.*, 2011), to a would-be vertebrate predator (Lloyd, 1973). In fireflies these defense glows are part of a multimodal aposematic signal syndrome: they simultaneously emit characteristic odors, described as musky, cabbage-like, fungus, peppermint and/or resin odors in different lampyrid species, reminiscent of the description of pyrazines (DeCock, 2009), which were identified as the volatile compounds of *Photuris trivittata* and associated with lower rates of ant predation, but without effect on vertebrates (Vencl *et al.*, 2016).

(2) *Prey attraction (intended receivers: potential prey)*. Prey attraction with light likely exploits a natural tendency of many insects and other animals to orient towards light, but it can also expose the light-emitting species to its own predators (Lloyd, 1983; Haddock *et al.*, 2010). Bioluminescent elaterid beetle larvae (*Pyrearinus termitilluminans)* excavate an intricate network of tunnels in the outer layers of Brazilian termite mounds, and use these as vantage points to attract and catch flying termites and ants with their green bioluminescence (Costa and Vanin, 2010). Among dipterans, the carnivorous larvae of species in three genera of fungus gnats (Mycetophilidae) use their bioluminescence to attract prey and trap them in their mucus webs that are covered with sticky or poisonous droplets (Sivinski, 1982, 1998; Viviani, 2002). Although mostly untested, many possible examples of prey attraction with light exist in marine environments, including octopods and many fishes (e.g., angler fish, dragon fish, hatchet fish) that seem to use light to lure in prey (**Fig. 4(A)**).

(3) *Reproduction (intended receivers: potential conspecific mates)*. There is limited information on the use of bioluminescence for mate attraction in the ocean (Herring, 2007). A few examples include the bioluminescent interactions of male and female ponyfish with male species-specific luminescent signaling (Sparks *et al.*, 2005), and the species-specific male courtship displays of cypridinid seed shrimp (ostracods; Cohen and Morin, 2003). Some marine species exhibit sexual dimorphism of light-producing phenotypes, suggesting a use in mate-attraction (reviewed in Ellis and Oakley, 2016). In contrast, mate attraction is a well-characterized function of adult bioluminescent signaling on land. For example, fungus gnat females are luminous, even though they do not eat, suggesting that they use their light to attract males. This is supported by adult males orienting towards pupal and female lights, and numerous males clinging to and fighting over female pupae, waiting for them to eclose; if no male is attached at the time of eclosion, adult females may flash their light on and off until a male arrives (Sivinski, 1982, 1998). Among beetles, flashes are exclusively used by lampyrids (fireflies), and glows are used by lampyrids, phengodids (railroad worms), elaterids (click beetles), and rhagophthalmids (Asian glow worms) for mate attraction by one or both sexes (**Fig. 4(B)**). There is compelling evidence that the origin of bioluminescence as a sexual signal is associated with higher species abundance and speciation rates across animals both on land and in the ocean (Ellis and Oakley, 2016).

Signal structure and function

As in other signal modalities, specific light signal characteristics are associated with signal function and/or signaling environment. For example short signals (i.e., flashes) with a sudden onset and high intensity are often used to startle potential predators, while longer signals (i.e., glows) that allow the receiver to localize a stationary sender are often used to attract prey and potential mates. Continuous glows from moving senders may often be advantageous in environments such as forests, where intermittent flashes, temporarily obscured by vegetation, can reduce signal detection efficiency by a receiver. However, in predator-rich environments, continuous glows may also significantly increase the predation risk of signaling animals and it is likely that the intermittent luminescence in fireflies evolved under predation pressure (Lloyd, 1989).

When signals are not generated within animals, but outside the body in bioluminescent secretions, as is the case for many marine animals, the limitations imposed by predators on signal traits are relaxed, or even may be reversed. Releasing a big, lasting

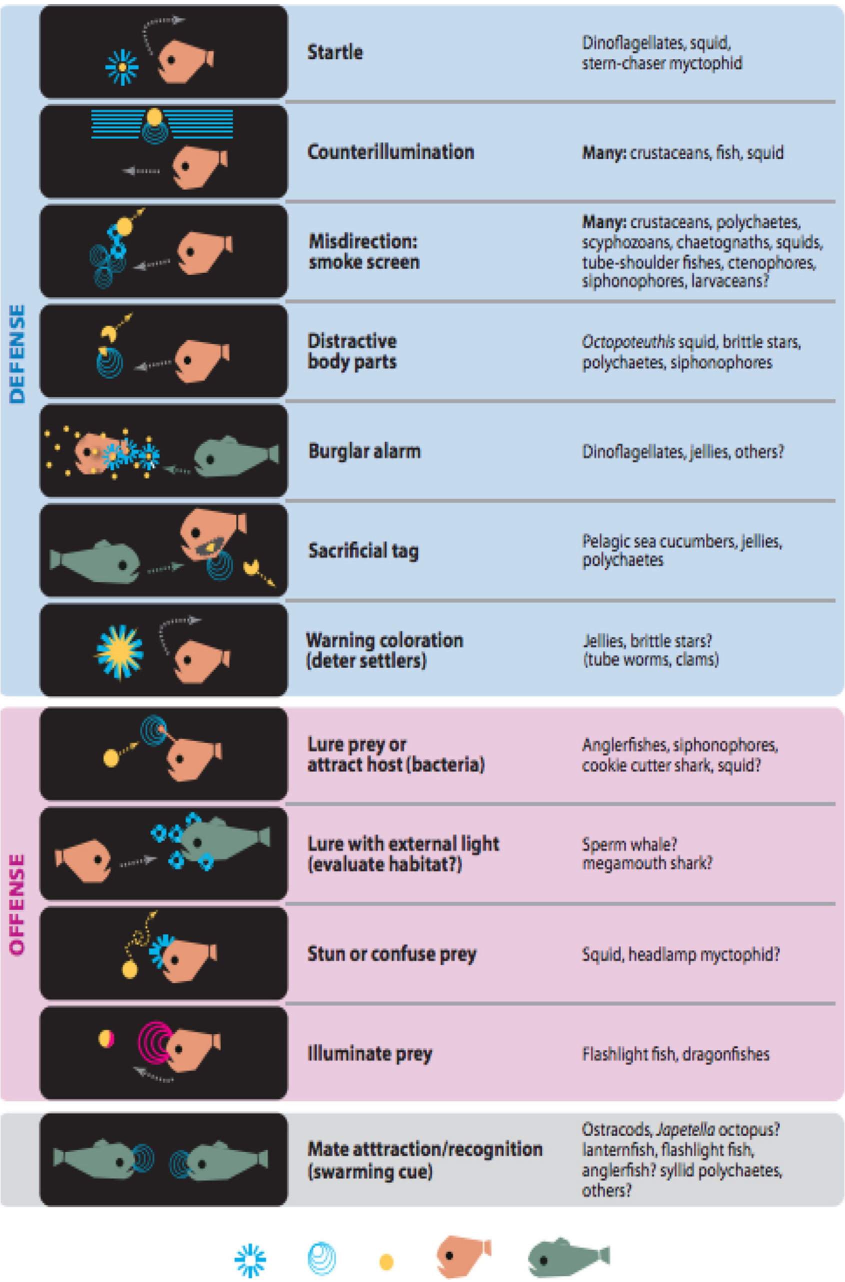
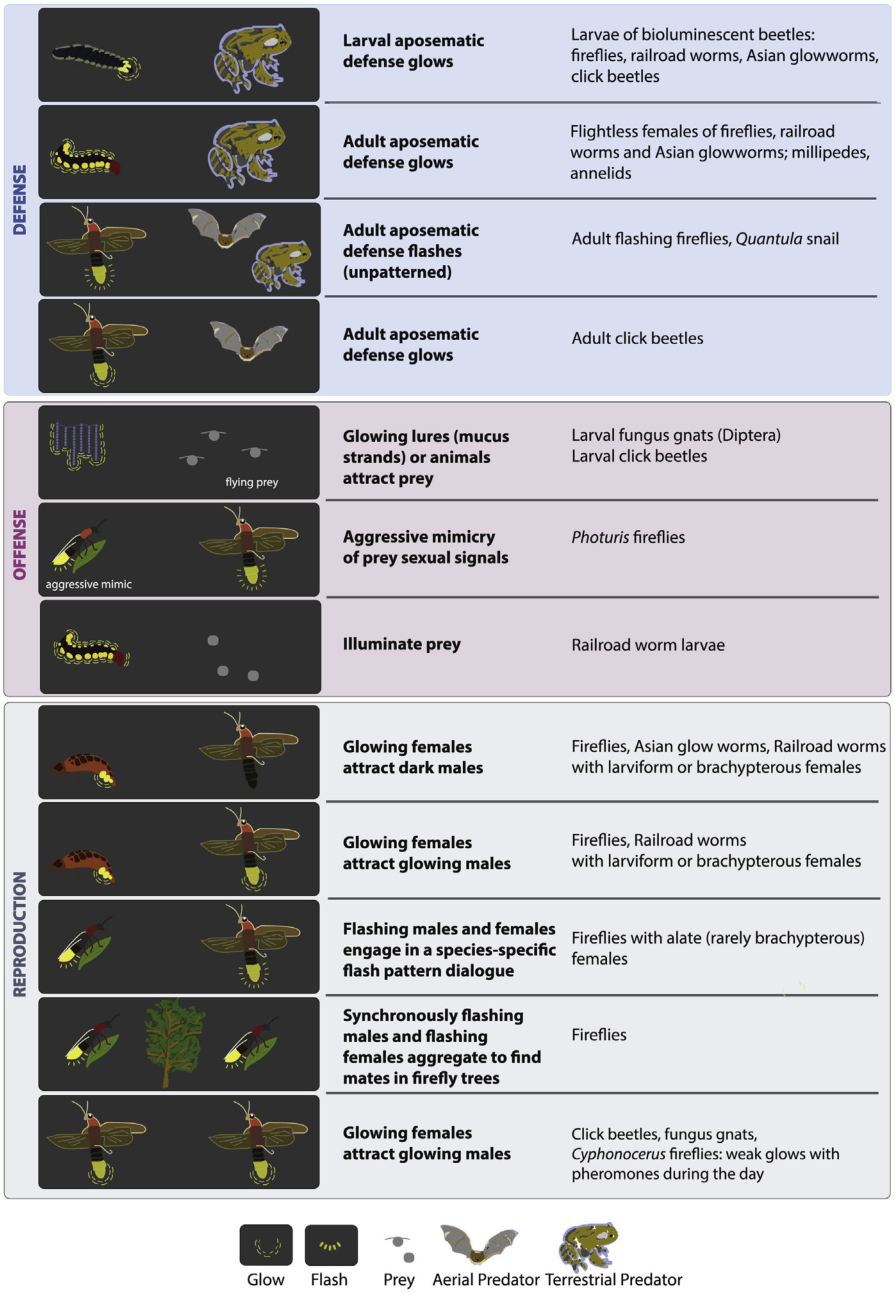


Fig. 4 Hypothesized functions of (A) (top): marine bioluminescence. From Haddock, S.H.D., Moline, M.A., Case, J.F., 2010. Bioluminescence in the sea. Annual Review of Marine Sciences 2, 443–493, and (B) (bottom): terrestrial bioluminescence in the contexts of defense (blue), offense (magenta), and intraspecific communication (gray). The organisms benefiting from these are listed to the right in each panel. Some animals are known to use their luminescence in several different roles.



DEFENSE	**Larval aposematic defense glows**	Larvae of bioluminescent beetles: fireflies, railroad worms, Asian glowworms, click beetles
	Adult aposematic defense glows	Flightless females of fireflies, railroad worms and Asian glowworms; millipedes, annelids
	Adult aposematic defense flashes (unpatterned)	Adult flashing fireflies, *Quantula* snail
	Adult aposematic defense glows	Adult click beetles
OFFENSE	**Glowing lures (mucus strands) or animals attract prey**	Larval fungus gnats (Diptera) Larval click beetles
	Aggressive mimicry of prey sexual signals	*Photuris* fireflies
	Illuminate prey	Railroad worm larvae
REPRODUCTION	**Glowing females attract dark males**	Fireflies, Asian glow worms, Railroad worms with larviform or brachypterous females
	Glowing females attract glowing males	Fireflies, Railroad worms with larviform or brachypterous females
	Flashing males and females engage in a species-specific flash pattern dialogue	Fireflies with alate (rarely brachypterous) females
	Synchronously flashing males and flashing females aggregate to find mates in firefly trees	Fireflies
	Glowing females attract glowing males	Click beetles, fungus gnats, *Cyphonocerus* fireflies: weak glows with pheromones during the day

Fig. 4 (*continued*).

cloud of glowing mucus into the environment when threatened by a predator likely increases the escape opportunities for the potential prey by extending the time before a predator can reorient and pursue the prey. For example many copepods release their bioluminescent chemicals from glands on the tail or swimming legs, which generate enough thrust during escape to eject the bioluminescence beyond the boundary layer of the escaping animal (Widder, 2002). As an advantage of secreted bioluminescence, the attackers can potentially be covered by the bioluminescent mucus, making them easy targets for secondary predators (Morin, 1986; Haddock *et al*., 2010; Widder, 2010). Similarly, when secreted signals are used as male location cues for females during mate attraction, the respective males usually do not move too far from their secreted signals, e.g., by swimming in tight spirals, rather than in straight lines (Rivers and Morin, 2008).

If signals are used for mate attraction and several species are active in the same area, sexual selection can cause these signals to evolve into complex, species-specific courtship displays that consist of temporal (flash duration, inter-pulse interval, flash pattern interval) and spatial (signaling area in environment and male movements while signaling) sequences of light-signals, as evident in the intriguing courtship displays of both male terrestrial fireflies (Lloyd, 1966) and male marine ostracods (Gerrish and Morin,

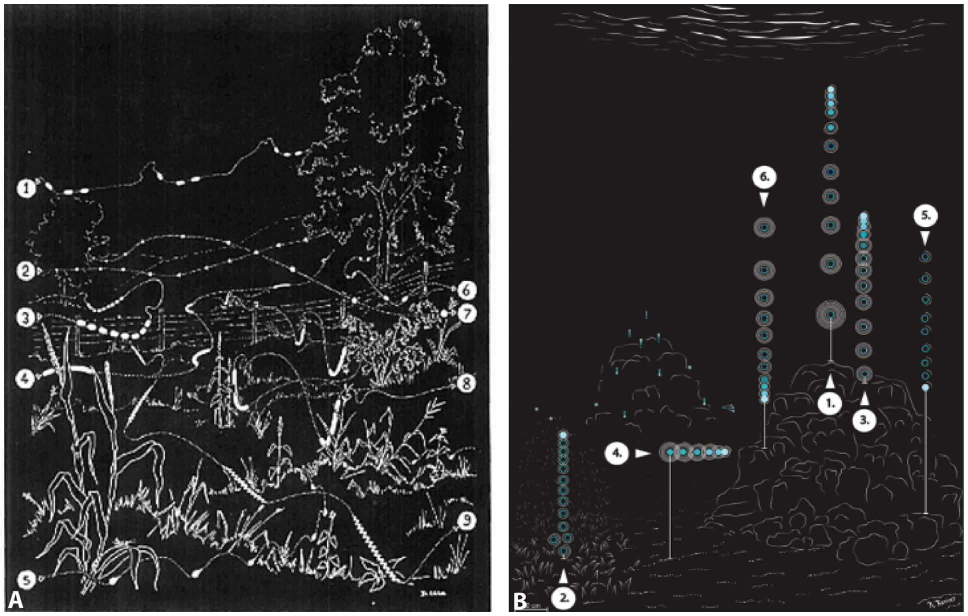


Fig. 5 Species-specific light signals of male fireflies and male ostracods, the two most thoroughly studied bioluminescent groups on land and in the ocean. These sexual signals are emitted as repeated flash patterns (fireflies) or pulses of bioluminescent secretions (ostracods) in space and time, and result in female flash answers (not shown) from sedentary firefly females, and approach behavior (without light signals) in female ostracods. In addition to the temporal and spatial signal variation among species, complex courtship behaviors can provide additional variation for sexual selection in both groups. (A) (left). Fireflies: (1) *Photinus consimilis* (slow-pulse), (2) *P. brimleyi*, (3) *P. carolinus*, (4) *P. collustrans*, (5) *P. marginellus*, (6) *P. consangineus*, (7) *P. ignitus*, (8) *P. pyralis*, (9) *P. granulatus*. (B) (right). Ostracods: (1) MWU, (2) *Photeros annecohenae*, (3) *Kornickeria hastingsi*, (4) MSH, (5) *Photeros morini* and (6) ZZD; relative signal duration indicated by *number of circles* surrounding the *center*. *Filled circles* represent pulses that would simultaneously be visible during the display based on signal durations (Gerrish, G.A., Morin, J.G., 2016. Living in sympatry via differentiation in time, space and display characters of courtship behaviors of bioluminescent marine ostracods. Marine Biology 163(9), 190; illustration by Natalie Renier).

2016), the two best-studied terrestrial and marine bioluminescent groups (**Fig. 5**). However, unlike the reciprocal duets seen in fireflies where females respond to males with species-specific response delays, female ostracods are not known to signal during courtship, rather they simply approach the displaying male. Behaviorally the ostracod system is similar to acoustic signaling in amphibians and insects, where "silent" females approach signaling males (Gerrish and Morin, 2016).

Neural control

In contrast to ostracods, which secrete their bioluminescent chemistry into the environment, fireflies retain neural control of their bioluminescent reactions (Timmins *et al*., 2001). Species-specific pattern generators are likely involved in generating the diverse courtship displays in both ostracods (secretion pattern) and fireflies (flash pattern) (Carlson and Copeland, 1985, Stanger-Hall and Lloyd, 2015). Variation in these neural controls would allow for evolutionary modifications of bioluminescent signaling behavior. Similarly, in brittle stars (echinoderms) a complex system of neurotransmitters modulates light output, with yet unknown function (Haddock *et al*., 2010).

Signal Detection: Brighter and High-contrast Signals are Detected More Easily

Light signals tend to be used in dark environments with brighter signals allowing for higher probabilities of detection, and at greater distances. Ambient light, moonlight, and low visibility due to particles in the ocean or in the air, interfere with detection of light signals (reducing the signal/light noise ratio) and can impact the bioluminescent signaling behavior of animals both on land and in the ocean. For example, firefly species change the onset of their bioluminescent signaling behavior in response to cloudy skies and/or moonlight (Lloyd, 1966), and ostracods only start signaling in the shallow ocean waters at astronomical twilight (~ 1 h after sunset) or near moonset, whichever occurs last (Morin and Cohen, 2010). Therefore, when required for efficient signaling, darkness becomes an ecological resource (Gerrish *et al*., 2009). Artificial lighting and wide-spread light pollution can reduce flashing activity in both ostracods and fireflies (Lloyd, 2006; Hagen *et al*., 2015; Gerrish and Morin, 2016; Owens *et al*., 2018) and it significantly reduces firefly mating (Ineichen and Rüttimann, 2012; Firebaugh and Haynes, 2016). When male *Aquatica ficta* fireflies, are experimentally exposed to higher levels of ambient light (<533 nm), they emit brighter signals, but with decreased frequency (Owens *et al*., 2018). However, longer wavelength ambient light (≥597 nm) did not affect signaling (Owens *et al*., 2018), thus replacing the widespread broad-spectrum white lights in urban areas with long-wavelength lights could reduce light pollution and support conservation efforts for fireflies and other nocturnal insects.

The role of bioluminescence color

In the open ocean, most emission spectra are blue (460–490 nm) and centered around the wavelengths that travels farthest through seawater (λ_{max}~470 nm); shifts towards green tend to be found in benthic and shallow coastal species, possibly because increased turbidity from particles in the water scatters blue light and favors the transmission of longer wavelengths (Haddock *et al.*, 2010; Widder, 2010). Interestingly, some squid change their light color with water temperature (Herring *et al.*, 1992), but the mechanism and functional relevance of this color change remains unclear. In contrast, the bioluminescent emissions in terrestrial environments are dominated by wavelengths in the green–yellow color spectrum, with some railroad worms and click beetles also emitting in the orange–red (Viviani, 2002). Bioluminescent signaling on land frequently occurs before total darkness (e.g., *Photinus* fireflies), therefore peak intensity wavelengths in the emission spectra (perceived as light color by the human eye) is expected to be under selection to enhance signal detection against the ambient light environment. One mechanism to improve signal visibility is to increase contrast against ambient light (contrast hypothesis: Lall *et al.*, 1980); another is to optimize the reflection of light signals off the signaling surface (Endler, 1992).

Signal Color

Light Color Contrast Against Ambient Light

Light-emitting fireflies (Lampyridae) are signaling under low ambient light conditions from approximately one hour before until several hours after sunset (complete darkness on moonless nights). The dusk-active firefly species in the genus *Photinus* likely evolved their early activity time in response to predation pressure by dark-active *Photuris* fireflies (Lloyd, 1984a). This makes *Photinus* fireflies an excellent study group for the impact of the ambient light environment on the evolution of bioluminescent signal color (Hall *et al.*, 2016). As the sun descends and sunset approaches, the terrestrial ambient light spectrum becomes dominated by longer wavelengths (Endler, 1993; Johnsen *et al.*, 2006). Species with earlier activity times (sunset) experience ambient light that is a mix of long wavelength (orange–red) light from the sky and shorter wavelength (green) light reflected off the vegetation. Species that signal after sunset experience reduced ambient light that contains relatively more short (blue) wavelengths. With increasing darkness the composition of the dim ambient light either goes to long-wave domination (without moon) or is spectrally neutral (full moon). This whole process (sun moving from $+10^\circ$ to -10° relative to the horizon) lasts ~1.3–2 h, depending on the distance from the equator.

Since the ambient light environment of twilight-active species is dominated by short (<550 nm: blue–green) and long (>600 nm: orange–red) wavelengths, a signal that is more yellow (550–600 nm) is expected to increase the signal-to-noise ratio against the green vegetation at this time, thus improving signal detection and facilitating mating success (Seliger *et al.*, 1982a,b; Endler, 1992). For later activity times, ambient light wavelengths become longer and lower intensity, and so the contrast hypothesis predicts either greener or no optimal light emission color in dark-active species. A recent phylogeny-based analysis of male flash color evolution in 24 North American firefly species showed that the males of twilight-active firefly species in closed habitats (surrounded by green vegetation) indeed tend to have yellower flashes (**Fig. 6**) than males of later active species, supporting the contrast hypothesis for light color evolution (Hall *et al.*, 2016).

Light Color Reflection off the Signaling Surface

Another mechanism to increase signal visibility is to reflect the bioluminescent signal off the background vegetation to amplify the light signal (Endler, 1992; **Fig. 7**). This reflectance hypothesis predicts that sedentary firefly females will produce greener light signals to maximize reflection off the green vegetation on which they signal, compared to the signals produced by conspecific airborne

Fig. 6 The males of firefly species active early and in habitats enclosed by vegetation are under selection to produce yellower bioluminescence, compared to firefly males flying over open fields with no back ground vegetation, or active after dark.

Fig. 7 Reflection of the light emission of a perched firefly from the vegetation. Photograph by Radim Schreiber, with permission (Fireflyexperience.org).

males. This is indeed the case for two of eight species with both male and female data: female light emissions were significantly greener than the light emissions of their conspecific males, supporting the reflectance hypothesis for these species (Hall *et al.*, 2016).

Light Color Dimorphism for Dual Function

Individuals of some species have more than one light organ, which in some cases emit different light spectra. The greatest known color difference within individuals is between the red and blue emissions of the suborbital and postorbital light organs of stomiatoid fishes (Herring, 1983). The blue emissions likely function in counter-illumination, while the red emissions could be used to spotlight prey or as a private channel for intraspecific communication without detection by other generally red-insensitive deep-sea animals; however, the rapid attenuation of red light in sea water makes intra-specific communication function unlikely (Widder *et al.*, 1984). A similar separation of spectral emissions between different light organs of the same individual occurs in phengodid beetles and click beetles (Herring, 1983). The dorsal lanterns of click beetles generally emit greenish glows when mechanically stimulated, suggesting defensive and possibly aposematic function, while the yellow-orange ventral lantern glows differ between species and are used during flight to attract potential mates (Lall *et al.*, 2010). The striking light color polymorphism between the dorsal and ventral light organs of the Jamaican click beetle (*Pyrophorus plagiophthalamus*) is under separate genetic control, with the luciferase in the ventral light organ showing signatures of selection (Stolz *et al.*, 2003).

The role of eyes

Firefly males have significantly larger eyes than their conspecific females in both diurnal and nocturnal taxa (Stanger-Hall *et al.*, 2018), supporting the importance of vision for airborne male navigation during mate search. Probably the most extreme case of sexual eye dimorphism in a bioluminescent species is found in the eyes of *Rhagophthalmus ohbai* (Rhagophthalmidae) with approximately 3000 facets in male eyes and 35 facets in female eyes (Lau *et al.*, 2007). This size dimorphism reflects differences in eye use: female *Rhagophthalmus* are larviform and emit a continuous glow to attract males, while males are able fliers, but not bioluminescent. Female eyes are likely used to detect ambient light to time their emergence for signaling, while male eyes are used for both airborne navigation at night and to detect female bioluminescence (Lau and Meyer-Rochow, 2006). This dual function of male eyes is beautifully reflected in male eye morphology: a smaller dorsal region has a maximal sensitivity to light of 600 nm, likely adapted to looking upward into the twilight sky for aerial navigation; the larger ventral region is maximally sensitive at 540–560 nm and facing downward to detect the yellow light emitted by larviform females.

Beyond eye size, the precise matching of visual sensitivity and bioluminescent emissions across firefly and click beetle species (Cronin *et al.*, 2000; Lall *et al.*, 2010), suggests strong sexual selection on both signal production (signal characteristics) and perception, as predicted by the sensory drive framework (Endler, 1993). The importance of vision for the detection of bioluminescent signals is also evident in the ocean. Among angler fish, only the free-living males of ceratid angler fish have large eyes to locate their bioluminescent females (Stewart and Pietsch, 1998), and the eyes of some copepods and non-luminous ostracods have semiparabolic reflectors thought to be adapted to the detection of bioluminescence (see Haddock *et al.*, 2010). With greater depths the prominence of bioluminescence increases relative to other visual stimuli, and below 1000 m the visual scene consists exclusively of point–source bioluminescent flashes, and the eyes of fishes match this change, becoming increasingly foveate and spatially acute with increasing depth, giving them excellent perception and localization of bioluminescent flashes (Warrant, 2000).

Signal Discrimination: Processing and Response

Once a bioluminescent signal is detected, it can be processed. Most processing is required for sexual signals, which require the identification of conspecific signals, possibly a signal response, and/or an approach towards a potential mate. The use and processing of complex courtship signals involves sophisticated neuronal control and processing for signal discrimination of conspecific from heterospecific signals (Wiley, 1983; Carlson and Copeland, 1985; Greenfield, 1994).

Among North American fireflies (~150 species in 16 genera) most species use flashes for elaborate courtship displays: airborne males engage in species-specific flashing behavior, while sedentary females wait in the vegetation for a conspecific male signal before they respond with a species-specific flash reply. If the detected signals match species-specific expectation windows in both males and females, this results in a flash dialogue and potentially in mating. For example, the searching males of the widespread "big dipper" firefly *Photinus pyralis* usually fly low (<1 m) above lawns (**Fig. 5(A)**) and emit single 600 ms long flashes at ~6.5 s intervals (at 20°C; flash intervals vary between 4 and 9 s depending on temperature in these ectotherms). *P. pyralis* females, perched on tall grass, have to respond at a delay of 2 s for the male to stay in the area and continue flashing (Lloyd, 1966). While flashing, *P. pyralis* females typically rotate and point their ventral light organ at the flashing male. Once a flash dialog ensues, the male will fly closer and eventually land close to the female, walk up to her while still flashing, and eventually make contact that includes intensive antennation behavior, likely sampling species-specific cuticular hydrocarbons to identify a conspecific mate (Ming and Lewis, 2010). Such elaborate signaling interactions are an excellent illustration of the complex signal processing that needs to take place to maximize reproductive success while minimizing mating mistakes and predation risk during bioluminescent courtship displays.

Minimizing false negatives versus false positives

Both ostracods and fireflies facilitate signal discrimination by dividing up the signaling space. Species may signal in different microhabitats, seasons, and/or time of night, however, it is not uncommon to encounter 6 or more signaling species in the same habitat, which poses a challenge for mate recognition (Morin and Cohen, 2010; Stanger-Hall and Lloyd, 2015). Both male and female response criteria to light signals are expected to be optimized between minimizing false negatives (not responding to conspecific signals) and minimizing false positives (responding to heterospecific signals, including potential predators). The initial response criteria for both males and females are expected to be somewhat flexible around a species-specific signaling window to not miss out on potential mating opportunities, especially in terrestrial habitats where signals may be partially obstructed from view by vegetation. For example, *P. macdermotti* firefly males emit a 2-flash flash pattern (**Fig. 7**), but after *P. macdermotti* females have seen the correct 2-flash male signal, they may respond to some single flashes (Lloyd, 1984b). However, as the dialogue proceeds, risking more false positives comes at a potentially significant cost of lost reproductive potential: (1) Most fireflies do not eat as adults and spend the resources obtained as larvae during mate search. (2) Males in species with elaborate courtship displays invest resources in the form of nuptial gifts during mating (South *et al.*, 2011), and mating mistakes can significantly reduce fitness. (3) Risking more false positives means a significantly higher predation risk for *Photinus* males by predatory *Photuris* females that mimic the flash response of *Photinus* females (**Fig. 3(B)**). For example, *Photuris versicolor* females can adjust their signal responses to attract males of four different *Photinus* species, and females seldom answered more than ten males without catching one (Lloyd, 1975), illustrating the strong selection pressure imposed by these predators on sexual signal recognition in *Photinus* males. Even if males hesitate, once they get close to the aggressive mimic, predatory *Photuris* females may switch from signal mimicry to another predatory tactic of intercepting males in the air, using the male flashes to aim their attacks (Lloyd and Wing, 1983). From an evolutionary perspective, males and/or female receivers should risk more false positives as they use up their limited resources or as sex ratios change and mating chances decline during the season. As a result, the "acceptable" response thresholds to signal variation for any firefly population are expected to evolve locally in response to the specific conditions in the respective microenvironment, including population size, sex-ratio, the number of sympatric heterospecific species, and the number of visually hunting and mimicking predatory species.

Evolution of male flash signal traits

The diversity in the male courtship displays of North American *Photinus* fireflies (**Fig. 8**) has been generated by both sexual and natural selection imposed by receivers. A phylogeny-based analysis showed that sexual selection acted on flash duration, resulting in character displacement between sympatric *Photinus* species, possibly reducing false positives. In addition, predation pressure by *Photuris* fireflies imposed natural selection on flash pattern intervals: *Photinus* species sympatric with more predatory *Photuris* species used longer dark intervals between successive male flash patterns, lowering the duty cycle (signal per time unit) of their signals and thus decreasing the information for predatory *Photuris* fireflies to predict their flight path and hawk them out of the air (Lloyd and Wing, 1983; Stanger-Hall and Lloyd, 2015). However, lowering the duty cycle of their courtship signals comes at a cost for firefly males, because firefly females respond preferentially to higher flash rates (Branham and Greenfield, 1996) and/or longer flash duration (Cratsley and Lewis, 2003). Thus the duty cycle of male flash signals in any *Photinus* population is expected to evolve in response to the specific local conditions, specifically conspecific female response preferences and numbers of sympatric, visually hunting and hawking predators.

Unintended Receivers: The Costs of Signaling

Sexual signaling may draw the attention of unintended receivers. This includes potential predators or parasites that may be "listening in" and using these signals as cues to locate and target the signaler (Endler, 1993). In addition to predatory *Photuris* fireflies (Lloyd and Wing, 1983), other predators that possibly specialize on fireflies include birds (Caprimulgidae, Nyctibiidae), spiders (Lycosidae, Araneidae), anoles (Iguanidae), and frogs and toads (Lloyd, 1973; DeCock, 2009; Lewis *et al.*, 2012). Parasitism by

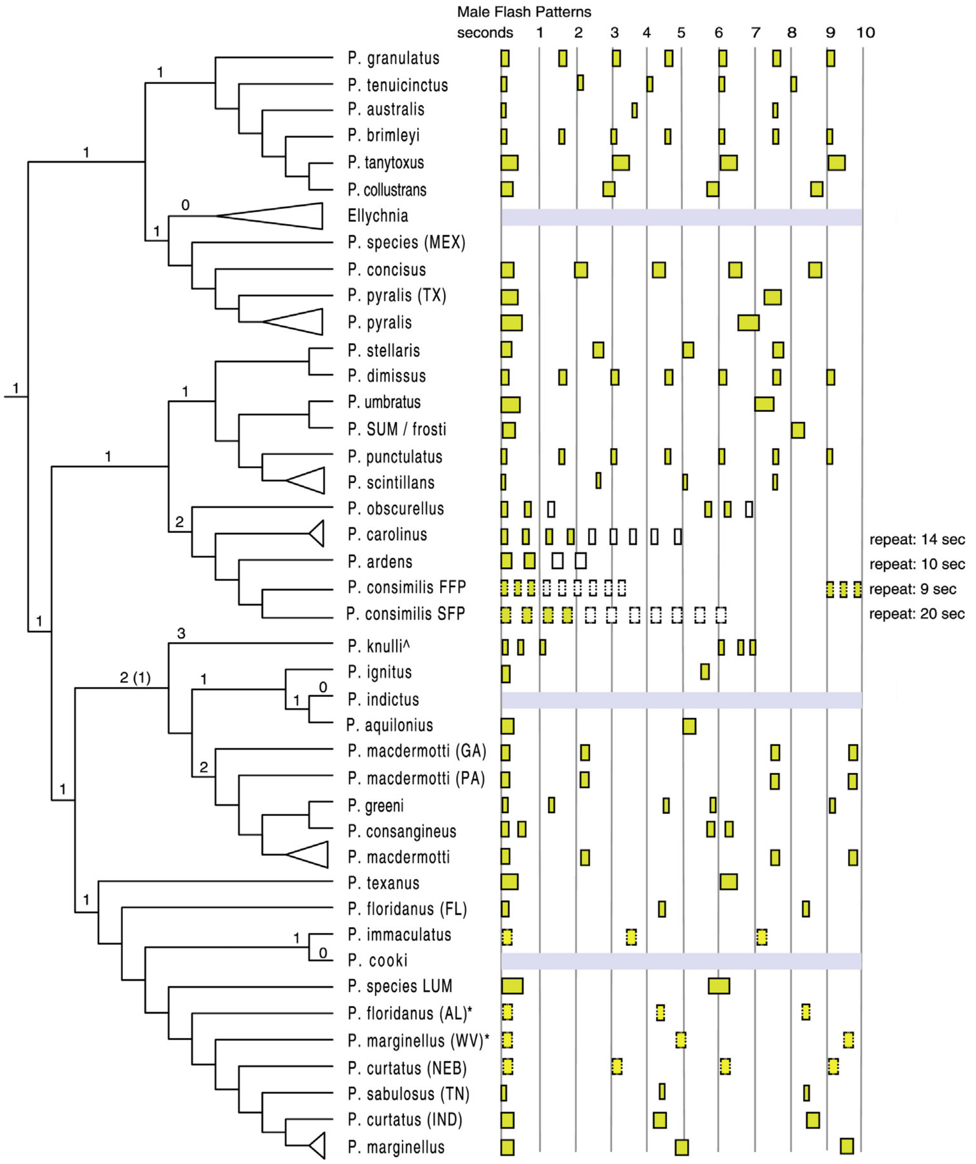


Fig. 8 The evolution of male courtship signals in North American *Photinus* fireflies. Typical flash patterns (adjusted for 20°C) are shown over a 10 s time period. Numbers on branches indicate the reconstructed ancestral number of flashes in a male flash pattern. Gray bars: loss of adult light signals and reversal to diurnal activity and pheromones as the main sexual signal. From Stanger-Hall, K.F., Lloyd, J.E., 2015. Flash signal evolution in *Photinus* fireflies: Character displacement and signal exploitation in a visual communication system. Evolution 69(3), 666–682).

phorid and tachinid flies, nematodes, hymenoptera and other parasites (Lloyd, 1973; Lewis *et al.*, 2012; Fallon *et al.*, 2018; Sivinski, 1998) are other costly consequences of bioluminescence signaling on land.

These visually orienting predators and parasites impose costs on flashing fireflies, and we expect selection to act on diminishing these cues (see above), sometimes leading to the loss of signals altogether (acoustic signals in crickets: Zuk and Kolluru, 1998) and/or switching to another signal channel (from light signals to pheromones) by becoming diurnal (Gronquist *et al.*, 2006). Field experiments have shown that continuous glows and higher signaling rates (duty cycles) significantly increased the likelihood of predation and staying dark was safest (Lloyd and Wing, 1983; Woods *et al.*, 2007), which may at least partly explain the three independent losses of bioluminescent courtship signals in *Photinus* fireflies (Stanger-Hall and Lloyd, 2015).

Summary

Researchers interested in the ecology and evolution of bioluminescent signaling are part of an exciting research field at the transition between (still ongoing) discovery of new and unexpected bioluminescence phenomena to the systematic study of a wide array of new research questions. Current multi-disciplinary approaches and research tools, including natural history, behavior, morphology, biochemistry, neurophysiology, genomics, transcriptomics and phylogenomics will help advance this research field and illuminate the proximate and ultimate causes of bioluminescent signal evolution in animal communication.

See also: **Communication:** Visual Signals Using Incident Light. **Neuronsand Senses:** Invertebrate Vision.

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