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13. Male Syrian hamsters weighing 120 g (Engle Laboratory Animals, Famersburg, Ind.) housed individually with food and water freely available were exposed to a 14:10 light:dark illumination cycle. Electrolytic lesions were produced in anesthesized hamsters (Nembutal, 75 mg per kilogram of body weight) by sterotaxically lowering an epoxylite-insulated insect pin electrode (exposed tip, 0.5 mm long; diameter, 0.37 mm), and delivering anodal d-c current of 1.5 mA for 10 seconds. Sham operations were performed by lowering the electrode to 1 mm above CMA or BLA coordinates without the delivery of current.
14. Adult ovariectomized female hamsters were made sexually receptive by sequential subcutaneous injections of estradiol benzoate (10 μg) and progesterone (200 μg) dissolved in 0.1 ml of sesame oil and administered 42 and 6 hours, respectively, before behavior testing. The female's receptivity was confirmed prior to mating behavior tests by exposure to a stud male.
15. Through the use of a microprojector, sections through each damaged CMA were traced onto a set of standard coronal sections through the amygdala (100-μm intervals). The proportion of damage to each nucleus of the amygdala on each side of the brain was calculated by an image analysis system (Quantimet 720) interfaced with a computer (PDP-11) to compare the summated area of the lesion with the entire area of that nucleus as represented on the standard sections.
16. Male hamsters with CMA lesions were ranked according to a score reflecting the severity of their mating deficit, that is, a score summated from the number of postoperative tests during which these animals displayed mounts and intromissions, but not ejaculations (+1); mounts, but not intromissions or ejaculations (+2); or a total absence of any copulatory behavior (+3). Rank order correlations were calculated between this ranking of mating deficit severity and a ranking of males with CMA lesions with respect to the proportion of bilateral damage to each nucleus in the amygdala.
17. Since the duration of mating tests varied between animals and between pre- and postoperative tests, we measured investigatory behavior as the time spent sniffing and licking each body region per minute of test. In animals with CMA lesions a decrease between pre- and postoperative investigation rates also reflected a significant decrease in the absolute amount of investigatory behavior [$T(16 = 22, P < .02$].
18. We calculated the percentage change from pre- to postoperative investigation rate of head, flanks, and anogenital area for each male. Rank order correlations were calculated between the decrease in anogenital investigation rate for each male with CMA lesions and the proportion of bilateral damage to each nucleus in the amygdala.
19. While vomeronasal input from the accessory olfactory bulb reaches the medial nucleus directly, olfactory input may reach the medial nucleus indirectly, by way of intra-amygdaloid afferents from olfactory projection areas of the amygdala [J. E. Krettek and J. L. Price, *J. Comp. Neurol.* **178**, 255 (1978)] or by way of afferents from other olfactory-related areas of the ventral forebrain (*5*).
20. Between 10 and 20 μCi of [^{3}H]proline or [^{3}H]leucine (specific activity, 40 to 60 Ci/mmole New England Nuclear) in 0.10 to 0.20 μl of physiological saline was injected bilaterally into the main and accessory olfactory bulbs through a 5-μl Hamilton syringe with a 26S-gauge needle. After a 48-hour survival period, the animals were perfused, and the brains were removed and cut 25 μm thick on a freezing microtome. Coronal sections at 200-μm intervals were mounted, coated with emulsion (Kodak NTB-2), and exposed for 2 to 3 weeks in the cold (2°C). The slides were developed (Kodak D-19) and counterstained with cresyl violet.
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27. We thank W. Brudon for providing illustrations and G. A. Kevetter for her collaboration during the initial stage of this project and for providing histological assistance. This work was supported by NSF research grant BMS 75-08595 to E. S. Valenstein, by NIH grant NS 14071 to S.S.W., and by national research service award 5 T32 MH14279-05 from the National Institute of Mental Health.

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Ecology of Colors of Firefly Bioluminescence

Abstract. *Dark-active North American fireflies emit green bioluminescence and dusk-active species emit yellow, in general. Yellow light and yellow visual spectral sensitivity may be adaptations to increase the signal-to-noise (that is, foliage-reflected ambient light) ratio for sexual signaling during twilight. The peaks of the electroretinogram visual spectral sensitivities of four species tested, two dark- and two dusk-active, correspond with the peak of their bioluminescent emissions.*

Firefly sexual signaling involves species-specific male flash patterns and coded time delays in female flash responses (*1*). Provided that there is sufficient light flux received in the region of the firefly visual spectral sensitivity, the precise color of the bioluminescent flash is not a factor in identification between males and females (*2*). Until now there has been no explanation proposed for the range of species-specific colors of bioluminescence from green through orange (λ_{max} = 546 to 594 nm), as determined by spectrophotometric measurements of the light organs of live fireflies (*3*). Since the use of bioluminescence as a signaling adaptation arose of necessity subsequent to the evolution of vision (*4*), it would be expected that the peaks of the bioluminescence emission spectra (*5*) would correspond with the peaks of visual spectral sensitivities for various species.

Bioluminescence cannot compete with ambient sunlight intensities, and therefore its evolution as a communicative mode in diverse species is associated with dimly lit environments and circumstances (such as nocturnal, subterranean, deep-sea) (*6*). In Fig. 1 are plotted histograms of the peak wavelengths of spectrophotometrically measured in vivo bioluminescence emission spectra for 55 species of North American (temperate zone) fireflies for which the time of onsets of flashing activity are known from direct field observations. The data form two broad groups: "early-starting" species, that is, those beginning flashing activity in advance of 30 minutes after sunset, and "late-starting" species, beginning after this. The determination of "early" or "late" was made from field records and the observer had no knowledge of the peak wavelengths of bioluminescence emission. There is a high degree of statistical significance of this correlation of peak wavelength of bioluminescence with time of beginning of flashing activity. Of 32 dark-active species, 23 emit green light ($\lambda_{max} \leq 558$ nm) and 21 of 23 dusk-active species emit yellow light ($\lambda_{max} \geq 560$ nm). Closely related (sibling) species might be expected to have similar or identical bioluminescent colors. However, the early flashers exhibit the yellow color, while late flashers emit green: for example, *Photinus ignitus* (556 nm) late, *Photinus consanguineus* (562 nm) early and *Photinus macdermotti* (565 nm) early, *Photinus tanytoxus* (555 nm) late, *Photinus collustrans* (560 nm) early.

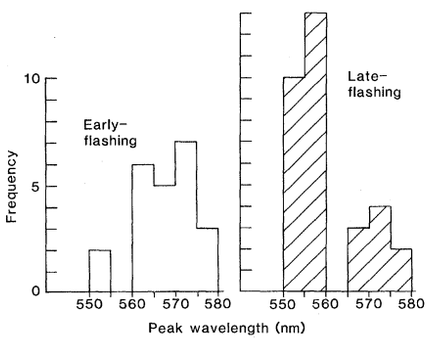

Fig. 1. Histograms of the peak wavelengths of the in vivo bioluminescence emission spectra from 55 species of North American fireflies. The wavelength intervals are arbitrarily 5 nm wide. The crosshatched area is representative of dark-active (*Late-flashing*) fireflies. The open area is representative of dusk-active (*Early-flashing*) fireflies. For each species the number of individuals measured ranged from 4 to 12.

Absorption bands of visual pigments are broad and have a significant degree of overlap with one another. Most visual pigments can be described by the Dartnall nomogram or by Ebrey and Honig nomograms (*7*). The electroretinogram (ERG) spectral sensitivites of the compound eyes (*8*) of two dark-active and two dusk-active firefly species were de-

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termined from dark-adapted intact preparations (upper panels of Fig. 2, A and B) and compared with the bioluminescent emission spectra (lower panels of Fig. 2, A and B). In all cases, for dark-active green-emitting *Photuris* (*lucicrescens* and *versicolor*) and for dusk-active yellow-emitting *Photinus* (*pyralis* and *scintillans*), the peak of the bioluminescence emission is identical with the peak of the visual spectral sensitivity. The green visual spectral sensitivity curves match the Ebrey-Honig nomograms. However, the yellow visual sensitivity curves are much narrower than the Ebrey-Honig nomograms, resulting in a depressed sensitivity in the green ($\lambda \simeq 500$ to 525 nm) by a factor of 50 compared with green-sensitive *P. lucicrescens* and *P. versicolor* (upper panels of Fig. 2, A and B).

From the range of wavelengths of Fig. 1 there is a minimum of eight distinct wavelength regions where differences in bioluminescence colors and in visual spectral sensitivities are statistically significant (9). Therefore, for the four species tested, the probability that the agreement between bioluminescence colors and ERG spectral sensitivities is fortuitous is $(1/8)^4 = 2.4 \times 10^{-4}$. The green visual spectral sensitivity curves (Fig. 2, *P. lucicrescens* and *P. versicolor*) have the usual Dartnall nomogram shapes of visual pigment absorption curves and are within the range of insect spectral sensitivity (*10*). We suggest that the yellow visual spectral sensitivity in *P. pyralis* and *P. scintillans* is an adaptation to maximize sensitivity to bioluminescence when green foliage-reflected light intensities are high, in temperate regions where twilight periods have significant lengths. A second selective advantage accrues for signal detection during dusk activity to yellow bioluminescent over green bioluminescent fireflies. A third selective advantage would be to evolve narrow yellow visual sensitivity. This narrowing, biasing against green sensitivity, is stronger evidence for adaptation to increase the ratios of bioluminescent signals to green ambient light, than even the correspondence between yellow bioluminescence and yellow visual spectral sensitivity. It is a fine tuning of the yellow visual spectral sensitivity for further biasing against noise—the background green foliage-reflected light.

The distinction made in this report between early-yellow and late-green is necessarily oversimplified. The bioluminescence emission of firefly species, evolving in the presence of changing ambient spectral intensities during twilight, should exhibit a complete range from green to yellow, depending on the specific time periods of their flashing activities and on the reflectance properties of their habitats (*11*). A number of aspects of this hypothesis remain to be tested. For example, seven of the nine exceptions to late-flashing green emission are salt-marsh, wet prairie species. The precise ERG spectra and habitat and time-specific ambient spectral intensitities of these species should be measured. In addition, comparisons should be made for

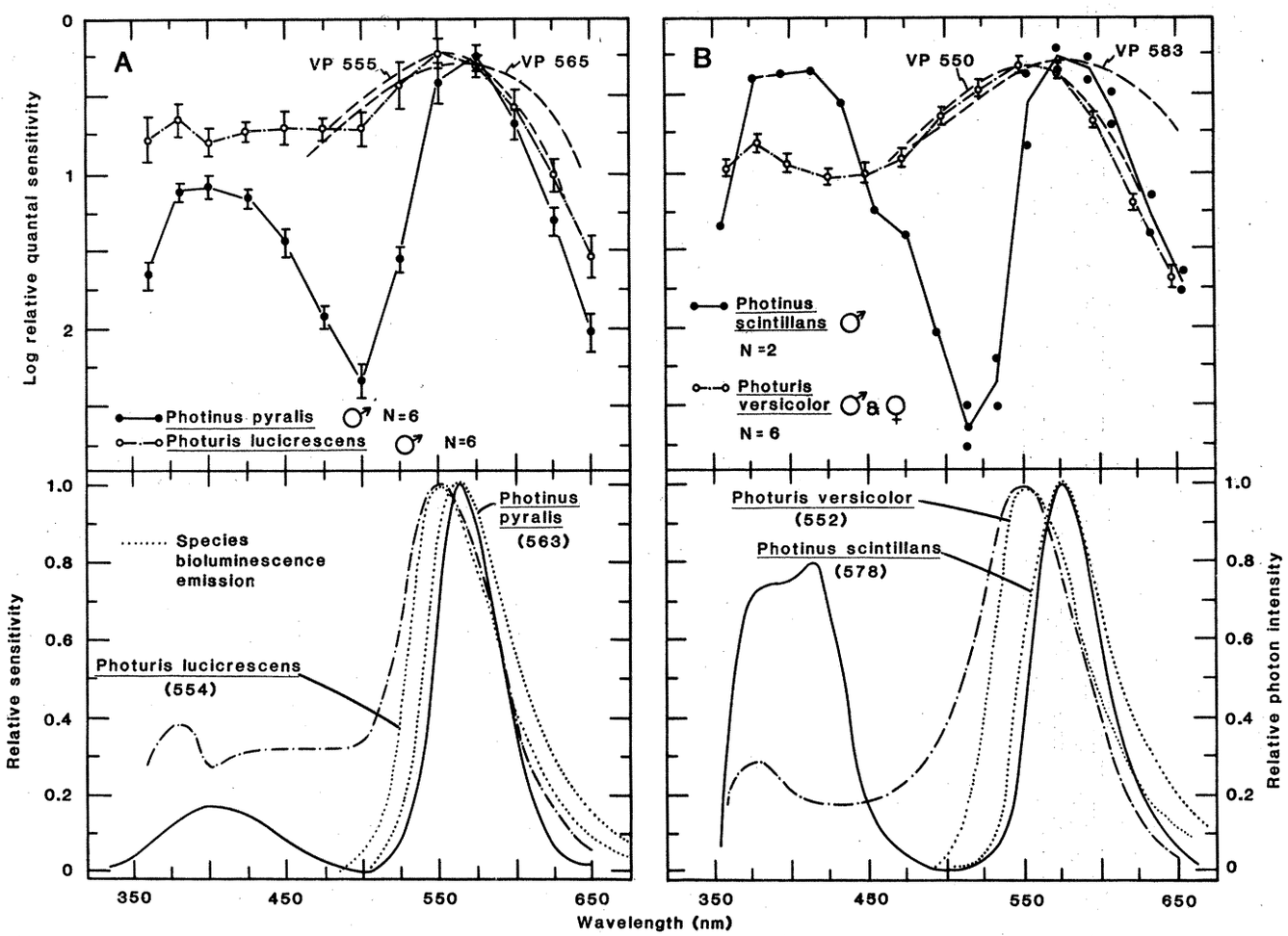

Fig. 2. A comparison of electroretinogram (ERG) spectral sensitivities and bioluminescence emission spectra for four firefly species. (Upper panels) Log of the relative quantum sensitivity plotted as a function of wavelength for the corneal 0.5-mV-amplitude ERG in dark-adapted intact eyes. The dashed lines represent Ebrey and Honig nomogram curves for pigments with λ_{max} at the observed peak wavelengths. The error bars represent ± 1 standard deviation. (Lower panels) Superposition of the relative photon intensity of species bioluminescence emission spectrum (dotted lines; the peak position is indicated in parentheses) and the ERG relative spectral sensitivity.

bioluminescent and nonbioluminescent Lampyridae, active at dusk. However, the present combination of electrophysiological, spectroscopic, and field behavioral data strongly support the hypothesis that the shift in color of firefly species bioluminescence and in visual spectral sensitivity from green to longer wavelengths is an evolutionary adaptation to increase the efficiency of sexual signaling in different, prevailing light environments.

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References and Notes

1. J. E. Lloyd, in *Bioluminescence in Action*, P. J. Herring, Ed. (Academic Press, New York, 1978), p. 570 and references therein.
2. Sexual responses can be elicited in the field from both sexes with various light sources (flashlights, with or without colored filters; cigarettes; matches; glowing light organs of other species) provided the stimulated signal has the correct timing and there is some portion of the spectrum of the artificial source that overlaps the effective visual spectral sensitivity.
3. The photon intensity for the bioluminescent flash is low, and for dark-adapted vision is below the threshold of human cones for precise color discrimination. Therefore spectrophotometric measurements in the field are essential for determining the color of the bioluminescent signal [W. H. Biggley, J. E. Lloyd, H. H. Seliger. *J. Gen. Physiol.* **50**, 1691, 1967; W. D. McElroy, H. H. Seliger, M. DeLuca, in *The Physiology of Insecta*, M. Rockstein, Ed. (Academic Press, New York, 1974), vol. 2, p. 411].
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6. J. E. Lloyd, in *How Animals Communicate*, T. Sebeok (Indiana University Press, Bloomington, 1977), p. 1128.
7. Dartnall (1953) proposed that the absorption bandwidth of all visual pigments when plotted on a frequency scale were identical, and independent of the absorption maxima of the pigment; he devised a constant bandwidth template now called the Dartnall nomogram. However, systematic deviations from this nomogram, with short wavelength pigments having broader bandwidths and longer wavelength pigments, narrower bandwidths, made Ebrey and Honig (1977) propose three different templates for pigments absorbing in the short, middle, and longer wavelengths [H. J. A. Dartnall, *Br. Med. Bull.* **9**, 24 (1953); T. G. Ebrey and B. Honig, *Vision Res.* **17**, 147 (1977)].
8. Sensitivity is the reciprocal of the quanta needed to evoke a criterion response. The details of the method, as well as the experimental set up are given in A. B. Lall, R. M. Chapman, C. O. Trouth, J. A. Holloway, *J. Comp. Physiol.* **135**, 21 (1980).
9. The standard deviation of an experimental determination of the peak wavelength of emission sion spectrum from a live firefly is approximately 1.2 nm (*3*), while that for the ERG spectral sensitivity determination in this work is 3 nm. Since, in the measurements reported here, the number of samples for each of the measurements ranged from $N = 2$ to $N = 12$ the 95 percent confidence limits for the specification of identity between an ERG peak and a bioluminescence emission peak are less than 2.3 nm.
10. All insects possess sensitivity maximums in the green (λ_{max} = 480 to 550 nm) [T. H. Goldsmith and G. D. Bernard, in *The Physiology of Insecta* R. M. Rockstein (Academic Press, London, 1974), vol. 2, p. 165]. Some butterflies [G. D. Bernard, *Science* **203**, 1125 (1979)] and the moth *Spodoptera exampta* [H. Langer, B. Hamann, C. C. Meinecke, *J. Comp. Physiol.* **129**, 235 (1979)] have additional red receptors.
11. The late flashing *Photuris aureolucens* (554 nm) in the same habitat initiates flashing activity 20 minutes earlier than its sibling species *Photuris caerulucens* (551 nm), while among the early flashers *Photinus macdermotti* (Maryland) (570 nm) initiates flashing activity earlier than *P. macdermotti* (Florida) (565 nm); *P. scintillans* (578 nm) in the same habitat initiates flashing activity 20 to 25 minutes earlier than *P. pyralis* (563 nm). There are no known reverse cases.
12. Research supported in part by Department of Energy contract EVO-3277 (to H.H.S.), NSF grant DEB 792-1744 (to J.E.L.), and grants from the Kettering Family Foundation and Robert L. Conway (to A.B.L.). Contribution number 1054 of the McCollum-Pratt Institute and the Department of Biology, Johns Hopkins University, Baltimore, Md.

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Induction of Suspension Feeding in Spionid Polychaetes by High Particulate Fluxes

Abstract. *The feeding behavior of three species of spionid polychaetes varied with water velocity. At moderate flows the worms ceased deposit feeding, formed their feeding tentacles into helices, and lifted them into the water column to capture material in suspension. This behavior was apparently a response to increased flux of suspended matter at high flows rather than to flow velocity alone. Organisms capable of switching their feeding behavior may be common in dynamically variable benthic environments.*

Deposit-feeding polychaete worms are a major group in soft-bottom areas of both the shallow and deep sea (*1*). These sediment-inhabiting annelids ingest food materials found on the sediment surface or within the sediment. Deposit feeders in general are considered to exploit a different food source than benthic suspension feeders, which obtain their food by removing it from the overlying water. Indeed, differences in factors controlling food supply are one explanation for the alternative development of predominantly deposit- or suspension-feeding benthic communities (*2*). Higher water velocities increase the flux of suspended materials, favoring suspension feeders, while removing fine-grained particulate matter from the sediment or preventing the deposition of this material, to the disfavor of deposit feeders.

A clear-cut distinction between these two feeding modes is probably unrealistic. Because there can be considerable resuspension of bottom materials by water currents in both the shallow (*3*) and deep sea (*4*), it could be advantageous for an animal to adjust its feeding behavior to utilize food in suspension or deposited on the bottom, depending on the

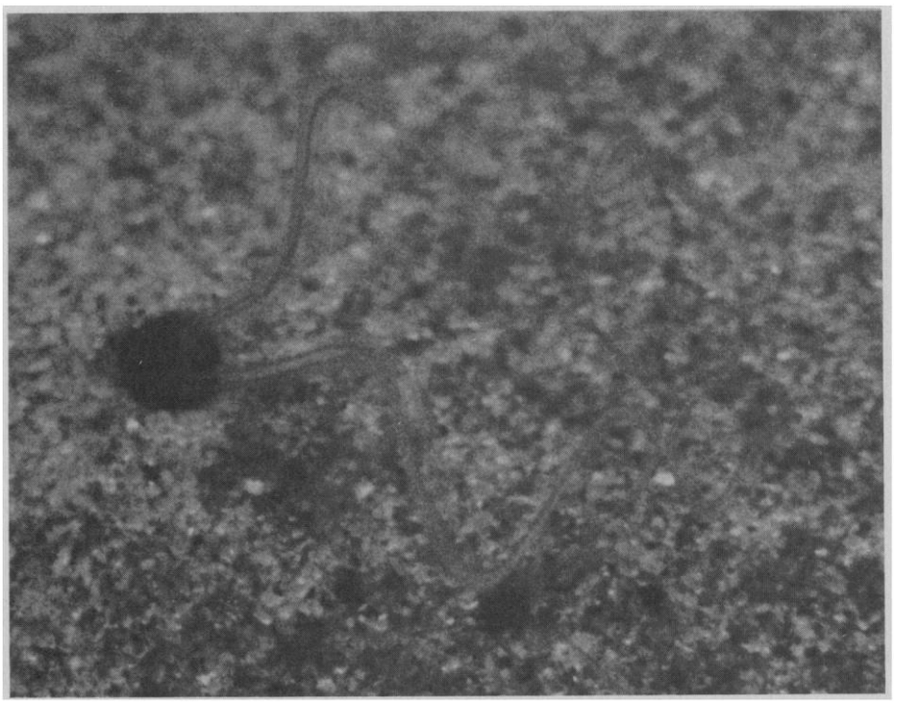

Fig. 1. Tentacles of *Pseudopolydora kempi japonica*, held in characteristic helical arrangement during suspension feeding. The current is moving from left to right at about 13 cm/sec (×4).

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