

A subline of the morphogenetic culture was established in 2,4-D medium with standard MS salts (12). Transfers to Cheng's MS-based medium (5) after 1 week produced a few abnormal embryoids. After 4 weeks in standard MS salts, transfers to Cheng's medium resulted in glossy green structures but not a single embryoid. N-amended salts maintain morphogenetic competence; standard MS salts allow embryoid formation and development.

From our results, the coordinate change in auxin level and nitrogen source is the key to triggering complete somatic embryogenesis in competent cultures of soybean. Although greater than 90 percent of the aggregates in our suspension can become green and "leafy" after transfer, not all give rise to well-formed embryoids. It may be that further reduction of the ammonium ion or other changes in the composition of the medium could lead to greater efficiency in embryoid production.

Change in auxin level alone can induce incomplete somatic embryogenesis from cell suspensions of a range of soybean cultivars and related species (6). This indicates that morphogenetic competence can be achieved in almost any soybean cell line. Progress to date on this cultivar of soybean suggests that a morphogenetic cell suspension can be established from our culture by a combination of further selection and further modification of the culture medium (7).

We hope that this procedure will prove useful in the establishment of morphogenetic suspension cultures of other large-seeded legumes. We know that embryos taken from young pea pods will make a hard glossy callus in response to the first step of the procedure; this callus appears very similar to the material we successfully manipulated in soybean.

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References and Notes

1. G. G. Henshaw, J. F. O'Hara, K. J. Webb, in *Differentiation "in Vitro" Proceedings*, M. M. Yeoman and D. E. S. Truman, Eds. (Cambridge Univ. Press, Cambridge, 1982), p. 231.
2. W. Wernicke, I. Potrykus, E. Thomas, *Protoplasma* 111, 53 (1982).
3. C. H. Chen, D. Songstad, A. Boe, *Bot. Soc. Am. Misc. Ser.* 162 (1982), p. 10.
4. S. L. Kimball and E. T. Bingham, *Crop Sci.* 13, 758 (1973); T. Kameya and J. Widholm, *Plant Sci. Lett.* 21, 289 (1981).
5. T. Y. Cheng, H. Saka, T. H. Voqui-Dinh, *Plant Sci. Lett.* 19, 91 (1980).
6. W. D. Beversdorf and E. T. Bingham, *Crop Sci.* 17, 307 (1977); G. C. Phillips and G. B. Collins, *Plant Cell Tissues Organ Cult.* 1, 123 (1981).
7. A. D. Krikorian and R. P. Kann, *Ann. Bot.* 47, 679 (1981).
8. F. C. Steward, M. O. Mapes, A. E. Kent, R. D. Holsten, *Science* 143, 20 (1964).
9. J. C. Chin and K. J. Scott, *Z. Pflanzenphysiol.* 85, 117 (1977).
10. K. A. Walker and S. J. Sato, *Plant Cell Tissues Organ Cult.* 1, 109 (1981).
11. T. Murashige and F. Skoog, *Physiol. Plant.* 15, 473 (1962).
12. P. Ozias-Akins and I. K. Vasil, *Protoplasma* 110, 95 (1982).
13. R. N. Konar, E. Thomas, H. E. Street, *Ann. Bot.* 36, 249 (1972).
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Nocturnal Aerial Predation of Fireflies by Light-Seeking Fireflies

Abstract. Female *Photuris* fireflies guided by their prey's luminescence attack flying fireflies at night. They sometimes use this hunting tactic together with prey attraction by mating-signal mimicry. Such predation could have been a major factor in the evolution of signaling behavior of American fireflies. Nocturnal aerial predation by an insect and attack guidance on energy emitted by airborne prey have not previously been reported.

Male fireflies seek mates by emitting luminescent signals as they fly about after dark (1). Although predation on searching males by bats and nocturnal birds has been reported (2), there has been no indication that males might be subject to heavy predation. Through three experiments with "airborne," light-emitting decoys that simulated male fireflies, we have found that female fireflies of several *Photuris* species are light-seeking, aerial predators (that is, "side-winder" hawkers). These predators are the only known nocturnal, aerial hunters among the insects, and the only hunters to use the energy emissions of airborne prey for attack guidance (3).

We flew light-emitting diodes (LED's) (4) covered with insect-sticking paste (5) from the tips of three 2.3-m fish poles that were slowly rotated (that is, swung from a hub; 120° apart) by a battery-powered motor (6) (Fig. 1). The decoys "flew" 1.3 ± 0.3 m above the ground and moved 0.24 or 0.48 m/sec. One LED glowed, one flashed (about 0.2-second duration) at 1-second intervals and one was unlit. A total of 33 *Photuris* females belonging to four species struck the glowing decoy, but the flashing and unlit decoys were not attacked (24 nights; nine sites; total running time, 34.7 hours). During two evenings (for 148 minutes) at one site, 21 attacks were made by females of one species, and in one instance three struck the same glowing LED within 2 seconds.

In the second experiment we trolled along a wooded roadside with a flashing, sticky decoy hanging on fine black wire from the tip of a 2-m fish pole (7). The decoy was held against the skylight to observe attacks. When an attacker was first seen, usually about 20 cm from the decoy, we made the decoy "hover" and do one of three things: stop flashing, continue flashing as before, or continue flashing and begin glowing dimly (8) in a manner simulating a firefly with a malfunctioning light organ, as sometimes seen in nature. (i) When the decoy stopped flashing incipient attackers flew away ($N = 11$). (ii) When the decoy continued flashing, incipient attackers attacked ($N = 10$) (Fig. 2), landed (flew into, then perched?) on the wire or pole up to 0.3 m from the decoy ($N = 13$), or flew away ($N = 7$). The ten that attacked took an average of 14.0 seconds to strike (9). (iii) When the decoy flashed and glowed incipient attackers struck the de-

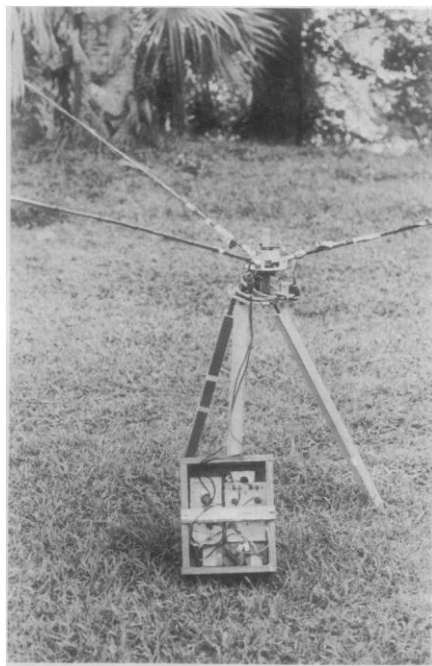


Fig. 1. Apparatus for flying sticky light-emitting diodes.

coy ($N = 23$) or the wire within 2 cm of it ($N = 2$) in an average of 4.6 seconds (10). In 13 additional cases of the second (flash, no glow) presentation and one of the third, two or more attackers appeared at the same time. (Since attacks on nonglowing decoys take longer, additional attackers have time to arrive.) Of these 30 fireflies, 4 attacked the decoy, 11 flew away, 6 landed, and 2 attacked other attackers. All attackers were females of *Photuris* sp. "D" (11).

In earlier studies on perched, hunting, signal mimics (12), *Photuris* females sometimes flew against the face or hand of the experimenter holding the flashing light. Suspecting that aerial attacks were being used in conjunction with aggressive signal-mimicry, we simulated the hovering, flashing approaches of "hesitant" males to perched, hunting, signal mimics. The decoys glowed dimly between flashes (see above, part iii of the second experiment). A total of 22 females of six species were tested where they were found in the field, and 17 of them attacked the decoy after as few as three flash presentations and usually within 1 minute (13). Females that began answering from within bushes sometimes changed perches after each response, moving out from their cover and toward the decoy before attacking. Twice females gave an appropriate female-mimic response to simulated male signals as they rose from their perches to attack, perhaps to slow the flight of targets. On four occasions females attacked a decoy that was approaching another female, and on four other occasions females were seen hovering near experimental flashes.

Finally, we attached living males to an LED decoy by means of a wire through the neck membrane. Attacking females ate the male, and when one male, by arrangement, slipped from the wire and fell to the ground, the attacker ate it there, apparently having "carried" it

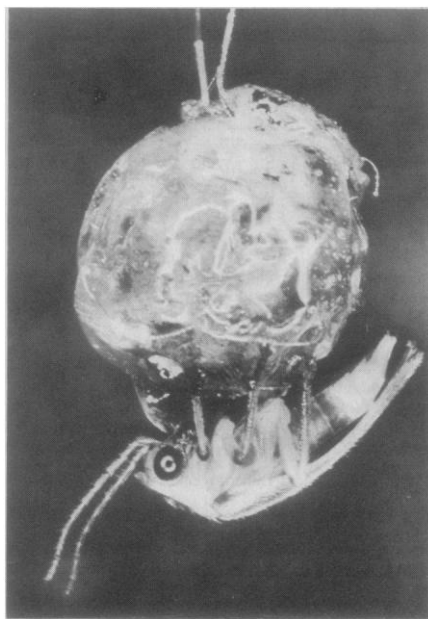


Fig. 2. *Photuris* species "D" female—with feet stuck to decoy she has just attacked. Decoy is an 8-mm bead with a light-emitting diode inside.

down. Once two females struck simultaneously and one ate the other, but in eight other cases in which *Photuris* females came in contact they immediately separated (14). We have observed presumptive hawkers hovering over *Photinus* and aggressive mimic females that were attracting males, and as many as six simultaneously following and flitting around flying, flashing males (15).

Photuris predation has probably been one of the more important pressures on firefly signaling in the New World, and many aspects of the signals and signaling systems of American species may have evolved in response to pressures from these versatile predators (16). The rarity of glow signals in males of American species and the hitherto inexplicable approaches of *Pyractomena* males of two species to answering females—after the first answer they drop to the ground

rather than flying closer to flash again (17)—are understandable in view of *Photuris* hawking. The techniques described here can be used to examine details of male signaling behavior, such as flight space, speed and maneuvers, and flash rate and form, for their significance in hawker avoidance. Actually, a natural, intercontinental experiment exists because neither *Photuris* nor predators like them are known from Asia and Africa, although fireflies abound.

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References and Notes

1. J. E. Lloyd, *Annu. Rev. Entomol.* **16**, 97 (1971); in *Bioluminescence in Action*, P. Herring, Ed. (Academic Press, New York, 1978), pp. 241–272.
2. ———, *Coleopt. Bull.* **27**, 91 (1973).
3. Insect orders with diurnal or twilight aerial predators include Odonata, Neuroptera, Mecoptera, Hymenoptera, and Diptera. Flying bats use sound energy from perched singers to aim attacks [M. D. Tuttle and M. J. Ryan, *Science* **214**, 677 (1981)].
4. Archer* 1320 G; Radio Shack, Home Office: 500 One Tandy Center, Fort Worth, Texas 76102.
5. Tack Trap*; Animal Repellents, Inc., Box 999, Griffin, Georgia 30224.
6. American 3255P; American Design Components, 39 Lispenard Street, New York 10013.
7. Speed, 20 cm/sec; flash, 0.2-second duration at 2-second intervals; wire, 0.12 mm in diameter.
8. About 5 percent of flash intensity: 1- to 4-mA current.
9. $\bar{x} = 14.0$, standard deviation (S.D.) = 14.1, range = 3.8 to 50; excluding the 50-second observation, $N = 9$, $\bar{x} = 10.0$, S.D. = 6.5, range = 3.8 to 20.0 seconds.
10. $\bar{x} = 4.5$, S.D. = 3.1, range 1.5 to 13.0 seconds.
11. J. E. Lloyd, in preparation.
12. ———, *Science* **187**, 452 (1975).
13. $\bar{x} = 23.7$ seconds, S.D. = 17.8, $N = 15$; two took 4 minutes.
14. One instance was captured on film (16-mm cinematic) by John Paling through use of an image intensifier.
15. S. R. Wing, thesis, University of Florida (1982); J. E. Lloyd and S. R. Wing, unpublished data.
16. J. E. Lloyd, *Annu. Rev. Entomol.* **28**, 131 (1983).
17. ———, *Coleopt. Bull.* **20**, 84 (1966); unpublished.
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