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24. Since c and b are the cost and benefit of the altruistic act, $c < 0$ and $b > 0$; h is the propensity with which heterozygotes perform altruistic acts.
25. Under the stated assumptions of this report, this expression equals the "adaptive function" [Eq. 53 of (*12*)] proposed elsewhere.
26. There is no internal equilibrium possible for this case ($0 \leq h \leq 1$). However, if there is overdominance so that heterozygotes are more altruistic than homozygotes ($h > 1$), then an internal equilibrium exists at $\hat{p} = h/(2h - 1)$ and it is stable if $-c/b < 1/2$. The existence of this equilibrium with strong selection has been confirmed [Eq. 49 of (*12*)].
27. This research was supported by NSF grant DEB-79 10191. We are grateful to M. Wade and S. Wright for criticism and comments.

27 May 1980; revised 1 August 1980

Male *Photuris* Fireflies Mimic Sexual Signals of Their Females' Prey

Abstract. Photuris *males emit flashed signals matching those of unrelated sympatric forms (*Photinus *and* Pyractomena *species). Some have only one flash pattern matching that of another species, others mimic at least two species, as well as emitting "their own" species-specific pattern. They tend to restrict the mimicking signals, but not their own, to the habitats, seasons, and daily periods of the mimicked species. Since* Photuris *females prey on males of other firefly species by mimicking their females' flashes, the* Photuris *males may be using their mimicry to locate and seduce their own hunting females. This mimicry is without known parallel in other animal communicative systems. It explains why the genus* Photuris *has been a frustrating mystery to taxonomists, who have long used flash patterns to distinguish sibling species in other genera.*

Fireflies of the American genera *Photinus, Pyractomena,* and *Photuris* (beetle family Lampyridae) use flashes of light for sexual communication. In general, flying males flash a species-typical pattern to which perched females of their species respond with a specific flashed answer. Males fly toward respondents and, after a few flash-exchanges, reach and mate with them (*1*). Numerous sibling species have been discovered through studies of male flash patterns (*2*). Females of the genus *Photuris*, in addition to using flashed signals in their own sexual communication, mimic females of other species, attract males, and eat them (*3*).

Barber (*2*) suspected that males of *Photuris lucicrescens* emit two distinct patterns. My field studies over the past 13 years show that, in addition to their own species-specific flashes, males of several *Photuris* species have two or more patterns (*4*) that mirror the patterns of males of *Photinus* and *Pyractomena* active at the same time and place. [Figure 1 shows model and mimic flash patterns (and the *Photuris*' own patterns).] This similarity probably evolved as a consequence of the aggressive mimicry of the *Photuris* females (*3*). Such a complex of behavioral mimicries is without known parallel in the animal kingdom.

Male flash pattern similarities are most obvious when they involve distinctive patterns, flickers with specific modulation rates (M rates), or flashes that are paired at specific time intervals. Most dramatic is the shifting back and forth by some *Photuris* males between their own species-typical pattern and the patterns of other species active at the same time and place. This report records and discusses this behavior in *Photuris* males (*5*).

In early spring in northwest peninsular Florida, males of an unnamed *Photuris* (VR) (*6*) mimic two species of *Pyractomena*: namely, *P. barberi* (short flickers) and *P. angustata* (minutes-long bright glows). Each mimicked species signals in pine and grassland less than 3 meters above the ground, while *Photuris* VR males produce a slow three- to seven-flash phrase (Fig. 1b) at much higher altitudes, especially around the crowns of pines. During the *Pyractomena* season, VR males descend into the *Pyractomena* flight space (*7*) and there emit flickers and glows closely resembling those of the *Pyractomena*. Individual *Photuris* males can often be seen to change their altitude and signaling pattern at the same time. Near the end of VR's season both *Pyractomena* are gone, and VR males then emit flickers and glows only occasionally. The M rate of VR's flicker is identical to that of *P. barberi* at comparable temperatures (Fig. 1, a and c; Table 1) (*8*).

Photuris AR (Florida panhandle) also mimics *P. angustata*'s glow in the appropriate space and season and otherwise emits its own single flash pattern at high altitudes (Fig. 1h).

At least five *Photuris* mimic the flicker of widespread and common *Pyractomena angulata* (Fig. 1, compare d with e, f, i, k, and l; Table 1). Three of these have their own distinctive pattern (Fig. 1, g, j, and n), but *Photuris* B emits only the mimicked pattern (Fig. 1e). The B females prey on *P. angulata* and at least two other species (*9*).

One of *angulata*'s mimics (in Maryland), *Photuris cinctipennis* (*10*), occurs in Florida and there emits its own pattern (Fig. 1n) (*11*), and mimics two *Photinus* (Fig. 1, p to u). Its mimicry is statistically indistinguishable from the model patterns in both cases.

Other examples of *Photuris* convergence on firefly associates include: (i) A flickering grassland *Photinus* in Colombia, South America, is mimicked by a *Photuris* that occurs with it, and its females have been observed answering the *Photinus* males (Fig. 1, v and w; Table 1). (ii) *Photuris jamaicensis* appears to mimic several *Photinus* in Jamaica, including some that are known prey of *jamaicensis* females (*12*), *P. evanescens* and *P. commissus* among them (Fig. 1, x to z; Table 1). (iii) *Photuris* A (Florida) emits a long single flash during the early evening activity period of its dusk-active associate and prey *Photinus collustrans*, and later switches to a one- to five-pulse pattern like that of another associate *Photinus lineellus* (Fig. 1, a′ and b′). Their patterns are statistically indistinguishable. (iv) Florida *Photuris versicolor*

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mimics its spring-associate *Pyractomena limbicollis* (Fig. 1, o and f') in season but later, after *limbicollis* is gone, emits only its own distinctive pattern (Fig. 1e'). (v) In upstate New York a *Photuris* (*pennsylvanica* s.s. ?) of wet meadows has its own distinctive flash-then-glow pattern (Fig. 1m), but for a few minutes at dusk it emits single flashes like those of twilight-active *Photinus curtatus* × *marginellus*, that occurs with it (Fig. 1, c' and d').

A number of other likely examples are known (*5*), but finally one may now wonder if the *Photuris* that Barber named *pyralomima* because of its flashing similarities with *Photinus pyralis* (*2*) is really a mimic of its namesake.

Table 1. Model and mimic flicker comparisons. Within the groups, the model is given first. In all cases, models and mimics are statistically indistinguishable (Mann-Whitney test, $P > .20$). *Pyractomena angulata* is model for several *Photuris*, and in each comparison flickers from appropriate temperature ranges were used. The M rate is the modulation rate in hertz; S.D. is the standard deviation; *N* is number analyzed, of flickers and of males. All recordings were of free-flying males in the field.

Organism	Temperature (°C)	M rate (Hz)		*N*	
		$\bar{x}$	S.D.	Flickers	Males
barberi	18°	8.6	.62	43	7
VR	19°	8.8	.62	24	9
angulata	20 to 22°	9.6	.42	16	7
B	21 to 22°	9.8	.37	23	10
angulata	18 to 20°	9.4	.77	29	13
tremulans	19 to 21°	9.0	.54	31	11
CR	19°	8.8	.27	6	3
angulata	19 to 20°	9.8	.62	13	8
Mo	20°	9.9	.04	2	1*
Colombia	22°	9.0	.37	20	14
Colombia	22°	9.1	.92	6	5
evanescens	21 to 22°	18.1	.53	65	37
jamaicensis	22°	17.1	.16	2	1*

*Statistical tests not made but observations within range of model values.

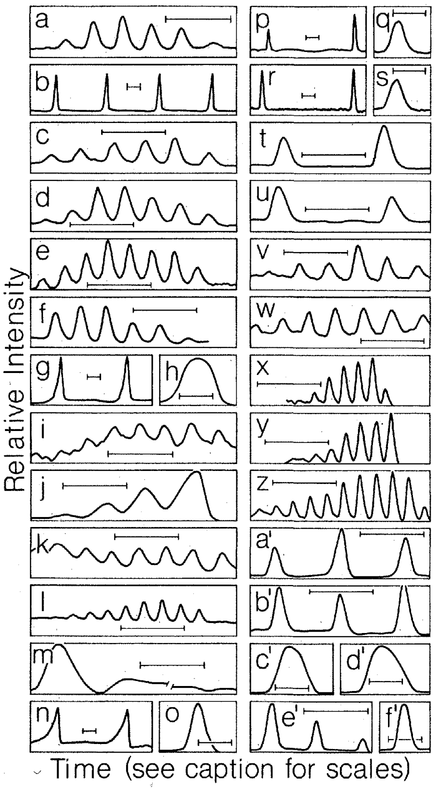

Fig. 1. Chart traces of flash patterns of flying male fireflies. The bars represent 0.25 second, except h, o, q, s, c', d', and f', where the bars represent 0.125 second (all are single, simple flashes). Recordings were made in the field with a photomultiplier magnetic-tape system. (a) *Pyractomena barberi*, 18.3°C (compare c). (b) *Photuris* VR's own pattern, 15.6°C. (c) *Photuris* VR flicker, 19.4°C. (d) *Pyractomena angulata*, 20.0°C (compare e, f, i, k, and l). (e) *Photuris* B, 23.3°C. (f) *Photuris tremulans*, 19.4°C. (g) *Photuris* Mo, 19.7°C. (h) *Photuris* AR's own pattern, 15.5°C. (i) *Photuris* Mo, 19.7°C. (j) *Photuris* CR's own (?) pattern, 18.9°C. (k) *Photuris* CR, 18.9°C. (l) *Photuris cinctipennis*, 25.0°C. (m) *Photuris pennsylvanica*'s own pattern, 13.6°C. (n) *Photuris cinctipennis*' (Florida) own flash, 21.7°C. (o) *Pyractomena limbicollis*, 18.6°C (compare f'). (p) *Photinus macdermotti* entire pattern, 22.2°C (compare r), and (q) individual flash at faster chart speed (compare s). (r) *Photuris cinctipennis*, 22.2°C, and (s) individual flash at faster chart speed. (t) *Photinus consanquineus*, 23.6°C (compare u). (u) *Photuris cinctipennis*, 23.6°C. (v) Colombian *Photinus* sp., 21.9°C (compare w). (w) Colombian *Photuris* sp., 21.9°C. (x) *Photinus evanescens* s.l., 21.7°C (compare y). (y) *Photuris jamaicensis*, 21.7°C. (z) *Photinus commissus*, 22.2°C. (a') *Photinus lineellus*, 26.2°C (compare b'). (b') *Photuris* A, 24.4°C. (c') *Photinus curtatus* × *marginellus*, 17.2°C (compare d'). (d') *Photuris pennsylvanica*, 13.6°C. (e') *Photuris versicolor*'s (Florida) own pattern, 21.7°C. (f') *Photuris versicolor* (21.7°C). Patterns paired here for demonstration were selected for clarity of form and, therefore, temperatures are sometimes not matched.

A number of possible explanations may be considered for this correspondence in male signaling (*5*). The similarities cannot be interpreted as the result of common evolutionary origin, and conservative descent for the genera involved are not closely related and indeed represent remote subfamilies. Their signaling similarities are too unusual and dramatic to be coincidental and, therefore, are surely the result of convergence. This convergence is too varied and precise to be the result of particular flight and flashing patterns being especially efficient under particular ambient conditions of vegetational structure, light, or other physical factors. There is at present no evidence for Batesian or other model-mimic relationships involving aposematism and nocturnal vertebrate predators such as bats or night hawks. Such mimicry is possible in certain instances, but unlikely in others, such as *Photuris* VR (*5*).

Females of mimicked species may sometimes answer the bogus signals of *Photuris* males. It is doubtful, however, that *Photuris* males have evolved their mimicry in this context, or even take such females as windfall prey. The *Photuris* males are vigorously competing for their own females, and females of mimicked species are almost always scarce (operational sex ratios are strongly male-biased).

Photuris males sometimes elicit responses from predacious females of other *Photuris* species, although because of seasonal isolation this is not expected with VR. Males of most *Photuris* have probably evolved to avoid such contacts because of the difficulty in preying upon such powerful females. In fact, these females and the risk they present may have been one of the more potent agents to shape the evolution of male search, signal-coding, and competition of American Lampyridae (*13*).

The females of the mimics' own species are undoubtedly the targets of the male mimicry, and the males are undoubtedly seeking mates. There may be important differences between the "strategies" of such species as VR, AR, and *jamaicensis*, in which males change from one signal to another, and those such as *Photuris* B that appear to have but a single pattern.

Among the possible explanations of the phenomenon as it occurs in *Photuris* VR are (i) hunting females (*femmes fatales*) that are sexually unresponsive may be located and raped. But the females are larger and more powerful than the males, and therefore the attempts are likely to be unsuccessful. (ii) Females may alternately oviposit and hunt over several days and, during this time, mate with two or more males. Mimicry could permit a male to locate a hunting female with marginal valence for hunting and change her to a mating condition (seduction-mimicry) [but see (*14*)]. On five occasions when mimicking males landed near flashes on the ground (all noted) they immediately began emitting the pulsing (treetop, nonmimic) pattern. (iii) Males that emit the prey-species pattern in the appropriate activity space and at the proper time may be demonstrating a trait that females favor. (iv) Males may indicate to females, by the patterns they use, the extent or nature of nutritional investment in progeny they are prepared to make. Thus, old males with low probability for survival to the next evening's mating flight might feasibly advertise their candidacy for cannibalism by a mate, this being the ultimate in nuptial feeding (*15*). Energetic and nutritive contributions are also possible through ejaculate (*15*), and the mimicked patterns could indicate the nature of the material the male has acquired from predatory activities.

In choosing among the above hypotheses I favor (ii) (for VR) because it is the simplest, appears stable evolutionarily, and pertinent observations seem to support it; however, a combination of (i) and (iv), a "kamikaze-copulation" as described for mantids (*16*), is also possible. More than one explanation may be involved.

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5. Additional data and details are in preparation.
6. Several unnamed *Photuris* spp. in my revisionary work are designated by letter.
7. VR's pulsing pattern is emitted up to 17 m with only 24 percent below 3 m, whereas 90 percent of its flickers and glows are emitted below 3 m, the space of the *Pyractomena* ($N = 607$).
8. Sustained glows, as in *angustata* and VR, are exceptional ("unknown") for species whose congeners flash, and are usually restricted to genera regarded as behaviorally primitive—for example, *Robopus* spp. in Jamaica and *Phausis* spp. in the eastern United States.
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10. *Photuris cinctipennis* flicker (25°C), $\overline{X} = 14.35$, standard deviation = 0.88, $N = 25$ flickers from 11 males. The single recording I have of *angulata* at a comparable temperature shows a rate of 12.5 Hz. Extrapolation of *angulata*'s rate-temperature regression indicates that the *cinctipennis* flickers were similar but not identical to those predicted for *angulata*.
11. Mark-release-recapture studies have not been made, but other evidence (such as transitional patterns at decoys) indicates that a single species emits the three patterns in Florida. It is possible that Maryland *cinctipennis* is a separate and sibling species. Regardless, these points are not critical to the phenomenon under consideration.
12. J. E. Lloyd, *Entomol. News* **80**, 169 (1969); E. G. Farnworth, thesis, University of Florida (1973).
13. If *Photuris* spp. were present in southeast Asia, they would end aggregative, sedentary mating systems of *Lucola* and *Pteroptyx* because males (and luminescing females) of these species are "sitting ducks." Similar behavior probably occurred in Western Hemisphere species before the evolution of *Photuris* predation. *Photinus pallens* of Jamaica does form sedentary aggregations, but it is larger than the resident *Photuris*.
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26 July 1979; revised 31 March 1980

Nonolfactory Sensory Pathway to the Telencephalon in a Teleost Fish

Abstract. *Pathways conveying lateral-line sensory information within the brain of a bullhead catfish terminate in a localized zone within the telencephalon. Thus, the telencephalon in teleosts, as in amniote species, contains regions that receive specific sensory input. Therefore, this lemniscal organization is not restricted to mammalian or amniote species but is a feature common to most, if not all, vertebrates.*

One concept of the evolution of the vertebrate central nervous system (CNS) is that in the "primitive vertebrate condition," the telencephalon was associated only with the olfactory apparatus. The evolution to the mammalian brain is viewed as a process of "encephalization" in which nonolfactory functions invade and finally dominate the telencephalon (*1*).

The brain of mammals and other amniote vertebrates contains a number of lemniscal channels, separate sensory pathways ascending from specific sensory nuclei in the brainstem to an ultimate telencephalic target (*2*). In mammals these telencephalic sensory target zones lie within the pallium, that portion of the telencephalon covering the lateral ventricle. The telencephalon of teleost fishes, however, lacks a neural pallium. Perhaps for this reason, a number of investigators have concluded that the telencephalon in teleost fish contains no specific sensory areas and acts instead as an "olfactory correlation" or "general arousal area" (*3*). However, recent evidence indicates that, at least for some elasmobranch fishes, information from nonolfactory sensory systems has access to the telencephalon (*4*). I undertook this study to determine whether one major nonolfactory sensory modality, the lateral line system, ultimately projects to a restricted area within the telencephalon of a teleost.

The primary sensory area for the lateral line system in fish lies within the rostral medulla (*5*). A prominent fiber bundle, the lateral lemniscus, leaves the primary lateral line sensory area, decussates, and ascends within the brainstem to terminate in the torus semicircularis of the mesencephalon (*5*). Until recently, higher order connections of the lateral line sense were largely a matter of conjecture on the basis of normal anatomical material. Many investigators have reported that the torus semicircularis provides a substantial input to the optic tectum (*6*). The tectum, then, was envisioned as a coordinating center for the various sensory modalities (*6*). Recent studies, however, indicate that the optic tectum is not the major target for the fibers arising in the torus semicircularis (*7*).

The bullhead catfish (*Ictalurus nebulosus*) was chosen for this study because it has a well-developed lateral line system comprising both mechanoreceptive and electroreceptive modalities. These modalities maintain separate CNS representations at both the medullary and mesencephalic levels (*5*). I dealt primarily with the connection of the mechanoreceptive component of the lateral line system.

Efferents of the torus semicircularis were determined by means of anterograde tracer techniques. A small quantity (20 to 30 nl) of tracer was injected un-

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