Aggressive Mimicry in Photuris Fireflies: Signal Repertoires by Femmes Fatales

Abstract. *Females of* Photuris versicolor *prey on males of other species by mimicking the flash responses of the prey's own females. They adjust their responses according to the male pattern, and attract males of four species with distinctively different flashed responses. The capabilities of the firefly brain are more complex than previously suspected. The mimicry is quite effective, and females seldom answered more than ten males without catching one.*

Females of at least 12 species of *Photuris* fireflies are predators of male fireflies of the genera *Photinus, Photuris, Pyractomena,* and *Robopus.* Evidence for this comes from observations of females eating (*1*) as well as capturing (*2, 3*) the males. The females lure the males to them by mimicking the mating signals of the prey species' females. The males are then seized and devoured. Although I have observed different *Photuris versicolor* females capturing males of four species, these observations do not alone demonstrate the mimicry versatility of these females since (i) *Photuris* species are difficult to identify and the behavior of different species could be attributed to a single one (*4*) and (ii) individual females might only be capable of mimicking the signal of a single prey species, variation among the females accounting for the inferred multiple mimicry. I have been able to demonstrate by field observation and experimentation on individual *P. versicolor* females that they do indeed have signal repertoires.

Females used for experimentation were found by their flashed answers to passing males or to penlight simulations of prey species' signals, and were on the ground or low vegetation. They were left in situ for experimentation. Experiments could not follow a rigid protocol because of the variable conditions under which the females were found. Also, since the experiments were conducted in the field, the females were continually influenced by the signals of free-flying males in the area. (On seven occasions experimental subjects interrupted experiments involving simulated patterns by flashing appropriate answers to different patterns that were emitted by passing males.) A female, once located, was first presented with an artificial flash pattern simulating the signal of one of the prey species. After several responses had been elicited, the pattern of another prey species was presented. Experiments were terminated if a female failed to respond to 15 to 20 presentations.

The species involved have a common general pattern of mating behavior. Males fly about in their habitat emitting their species-specific flashing pattern. Females flash answers from perches. Timing elements of the emissions are important for recognition. Important parameters in the male patterns are flash number, rate, and duration, and in the female response, flash length, and the delay at which it occurs after the male pattern. Advertising males repeat their patterns at characteristic intervals. When a male receives an answer to his signal he flies toward it and emits his pattern again. A flash-answer dialogue continues for five to ten exchanges and until the male reaches the female. Figure 1 illustrates the mating signal codes of the species involved (*5*), and tabulates the observed mimicry repertoires observed.

Two females were observed in natural "experiments" answering passing males of both *Photinus tanytoxus* and *Photuris congener,* and a third female answered a simulated *Photinus macdermotti* pattern and was found to be already eating a *Photuris* sp. *A* (*6*) male.

Eleven females answered the *macdermotti* simulation appropriately and then answered the *tanytoxus* simulation appropriately. This change required altering the length of their emissions as well as flashing after each flash rather than only after the second, as necessary for *macdermotti* (Fig. 1). For example, one female answered 11 consecutive *macdermotti* patterns with flashes 0.12 to 0.16 second in duration (at intervals of 8 to 10 seconds). On the first nine she flashed after each pulse of each pattern (*7*); she answered the next two correctly. She was then presented with several 0.5-second flashes (*tanytoxus*). She did not answer the first seven, but on numbers eight to ten responded with a short flash. On the 11th she produced a dim glow after the flash, and on the 12th her flash length was 0.6 second and the glow was held more than 9 seconds. She was then given the *macdermotti* pattern, which she answered properly on the first presentation, but with an intermediate flash length of 0.24 second (*8*) and no afterglow. Her next flash was 0.16 second in duration. In other words, she had immediately switched to the *macdermotti* response. Then, given a 0.5-second (*tanytoxus*) flash, she answered it with the appropriate long answer, a 0.6-second flash. In both cases she had made a rapid adjustment on the basis of the duration of the stimulus flash. Females sometimes responded immediately to pattern changes, but occasionally as many as 15 presentations had to be made before a response to the new signal could be elicited.

Six other females were given the simulated *tanytoxus* pattern first and then after one to eight presentations responded to the *macdermotti* pattern. One would not answer the *macdermotti* pattern and one always ($N = 15$) flashed after both pulses of the pattern. Fe-

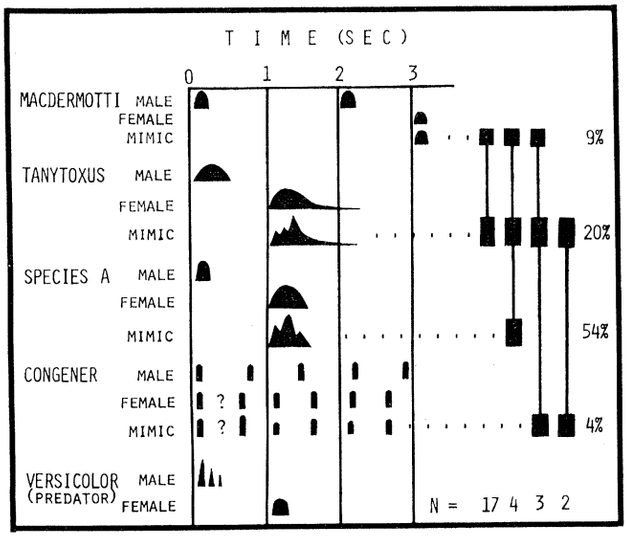

Fig. 1. Luminescent signals of fireflies. Response used by predator is shown below female answer it mimics. Vertical bars at right indicate observed individual repertoires; N is the number of females exhibiting the repertoire. Capture rates (percentages) are adjacent to prey species. The flash rate of the *congener* female is variable, and the specific nature of the coding is unknown (see text).

males occasionally stopped answering any pattern or flew away, and those tested undoubtedly differed with respect to age, condition of ovaries, number of successful predations, exposure to flashes of foreign males (kinds and numbers), and genetic makeup.

Apparently the mimicry is not perfect, although comparative figures cannot be given since attraction rates for conspecific interactions are unknown. One female captured the 12th *macdermotti* male she answered. Another answered 20 *congener* males, and then moved to a different perch several meters away and answered more than 20 additional males before she captured one. Another female caught the 21st *congener* male that she was observed to answer. Capture rates were higher for prey belonging to other species: on five occasions I observed the demise of *Photuris A* males; two females captured the first male answered, one caught the second, one the tenth, and one female got the 11th, although she had seized the seventh male and it had escaped. Two other females captured the fifth *tanytoxus* males that they answered.

What is the evolutionary origin of the false signals? Two independent sources are suggested. The flashed responses to *Photuris A, Photinus tanytoxus,* and *Photinus macdermotti* males appear to be similar in delay timing to the predator's own mating responses. False signals could have been derived originally from mating responses and subsequently modified. Responses to the flashes of *Photuris congener* males are similar to the flashes that the predaceous females, and those of many other *Photuris* species, commonly emit when they walk, land, or take flight (*9*). These "locomotion" flashes would need little if any modification to attract some *congener* males. (The flashes of the *congener* female, unlike those of other species, do not bear a specific relation to each flash of the male.) I am able to attract about one male in ten to the 0.08-second flashes of a free-running oscillator with a period like that of the males. I once observed a lycosid spider eating a *congener* male that continued to emit his rhythmic pattern; two additional *congener* males were attracted to the flashes of the captive, and were also seized by the spider. I offer this not as an example of a tool-using spider, for I doubt that it is repeated with regularity, but as an indication of how a physiologically inappropriate but trophically fortuitous activation of the locomotion flash mechanism by the flashes of a passing *congener* male could immediately put the female into the aggressive mimicry role. These observations indicate that the capabilities of the firefly brain are more complex than hitherto suspected.

JAMES E. LLOYD

Department of Entomology, University of Florida, Gainesville 32611

References and Notes

1. J. E. Lloyd, *Coleopt. Bull.* **27**, 91 (19 → L. L. Buschman, *ibid.* **28**, 27 (1974).
2. J. E. Lloyd, *Science* **149**, 653 (1965).
3. E. G. Farnworth, thesis, University of Florida (1973).
4. *Photuris versicolor* is a complex of several morphologically similar species which are widely distributed in the eastern and central United States. Extensive field investigations indicate that probably only one species is present in Gainesville.
5. The mating signals of prey species are discussed in more detail in J. E. Lloyd, *Univ. Mich. Mus. Zool. Misc. Publ. No. 130* (1966), pp. 1–95; *Fla. Entomol.* **52**, 29 (1969).
6. This *Photuris* is apparently a new species. Revisional studies and a Latin binomen will be reported at a later date (J. E. Lloyd, in preparation).
7. These interposed flashes were occasionally observed during actual predation of this species on *macdermotti* (*2*) and could be eliminated from the responses of some females when the stimulus patterns were spaced at intervals of 8 to 10 seconds.
8. Both 0.16 and 0.24 second are within the range of *macdermotti* flash responses. The 0.24-second flash was intermediate only with respect to the responses this female emitted.
9. J. E. Lloyd, *Entomol. News* **79**, 265 (1968).
10. I thank E. G. Farnworth and R. S. Lloyd for assistance in the field; T. J. Walker for helpful discussion, comments on the manuscript, and the loan of photographic equipment; A. Owens for photographic technical assistance; and the National Science Foundation (grant GB 7407) for financial assistance. Florida Agricultural Experiment Station Journal Series No. 5447.

16 August 1974

Erythrocytes in Human Muscular Dystrophy

The observations reported by Matheson and Howland (*1*) appeared to fill the need for a simple and reliable method for detecting heterozygous carriers of Duchenne muscular dystrophy (DMD). Dramatic surface deformation of erythrocytes in scanning electron micrographs was observed by these authors in both DMD patients and heterozygous carriers. This observation was consistent with previous results indicating possible abnormalities in cation transport (*2*), fatty acid patterns (*3*), and sphingomyelin levels (*3*) in erythrocyte membranes in human DMD, and also with abnormal erythrocyte morphology described in murine muscular dystrophy (*4*).

On the basis of these reports we studied the erythrocyte morphology in five individuals with DMD, three obligatory carriers, and two normal controls. The methodology was identical to that utilized by Matheson and Howland. Table 1 summarizes our findings and the data of these authors. Only one of our five DMD patients had a percentage of distorted erythrocytes falling just outside the normal range. All carriers demonstrated normal values. In addition, erythrocytes from DMD patients and obligatory carriers also exhibited normal morphology in routine peripheral blood smears stained with Wright's solution, normal osmotic fragility, and normal resistance to peroxide hemolysis.

Table 1. Comparison of results obtained by Miale *et al.* (this comment) with results reported by Matheson and Howland (*1*). Distorted red blood cells are abbreviated Dist. RBC's.

Miale *et al.*			Matheson and Howland		
Sex	Age	Dist. RBC's (%)	Sex	Age	RBC's Dist. (%)
		Normal controls			
M	32	0	M	43	3.4
F	38	1	M	45	3.3
			M	36	7.4
			F	32	4.0
			F	20	3.2
		Obligatory carriers			
F	42	6	F	32	35.1
F	39	5	F	37	39.9
F	37	0	F	32	34.0
		DMD patients			
M	13	5	M	12	65.4
M	11	0	M	15	98.4
M	10	0	M	14	40.6
M	9	24	M	1	20.6
M	6	7			

In summary, our data do not support the adequacy of scanning electron microscopic analysis of erythrocytes for the detection of heterozygous carriers of DMD.

T. D. MIALE, JAIME L. FRIAS
DANIEL L. LAWSON

Department of Pediatrics, College of Medicine, University of Florida, Gainesville 32610

References

1. D. W. Matheson and J. L. Howland, *Science* **184**, 165 (1974).
2. J. L. Probstfield, Y. Wang, A. H. L. From, *Proc. Soc. Exp. Biol. Med.* **141**, 479 (1972).
3. D. Kunze, G. Reichmann, E. Egger, G. Leuschner, H. Eckhardt, *Clin. Chim. Acta* **43**, 333 (1973).
4. P. F. Morse and J. L. Howland, *Nature (Lond.)* **245**, 156 (1973).

12 August 1974