OCCURRENCE OF AGGRESSIVE MIMICRY IN FIREFLIES

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ABSTRACT

Predation by aggressive mimicry in fireflies is known only in females of the *Photuris pennsylvanica-versicolor* group (it is doubtful that fireflies in the other group of the genus, i.e. *P. congener* and relatives, are predators as adults). Aggressive mimicry has been observed in 10 species, and circumstantial evidence suggests that such predation probably occurs in all species of the *pennsylvanica-versicolor* group, though there could be idiosyncratic exceptions. Probably most species prey on 2 or more species: *P. versicolor* preys on at least 11. Males and larvae of some *Photuris* spp. may also be aggressive mimics, but evidence is only suggestive.

RESUMEN

Predación por mímica agresiva en "fireflies" es sabido solamente en hembras del grupo *Photuris pennsylvanica-versicolor* (es dudoso que en el otro grupo del género de "fireflies", i.e. *P. congener* y sus parientes, sean predatores como adultos. Mímica agresiva ha sido observada en 10 especies, y evidencia circunstancial sugiere que tal predación probablemente ocurra en todas las especies del grupo de *pennsylvanica-versicolor*, aunque pudieran haber excepciones diferenciativas. Probablemente la mayoría de las especies son predatoras en dos o más especies: *P. versicolor* es predator por lo menos de 11. Machos y larvas de algunos *Photuris* spp. pudieron ser mímicas agresivas, pero la evidencia es solo una sugerencia.

Photuris firefly females flash-respond correctly to the mating signals of males of certain other species, attract the males and eat them (Fig. 1; Lloyd 1965, 1975, 1978). Williams (1917) and Hess (1920) both observed that it was male fireflies and not both sexes that were captured, and both correctly surmised that this was related to the different sexual roles during signaling and attraction. Hess "anticipated" the recent demonstration that *Photuris* females sometimes use their prey's light to aim attacks (p. 52, 53; see below; Lloyd and Wing 1983), and Williams, the occurrence of aggressive mimicry: "The fact that victims were always males . . . and that the feeders were invariably females, strongly suggests that the weak *Photinus* males were drawn to their untimely ends by the lure of the greenish-yellow light of the female *Photuris*." (p. 24). It is not possible to know with certainty what species Hess and Williams observed because, as Barber (1951) noted with emphasis, most species were then identified as *Photuris pennsylvanica* (a practice that continues today, 33 years after Barber, as a malpractice). From their descriptions of male flashing behavior I believe that they observed *P. versicolor*.

From his own field experience and the literature, in his monograph on *Photuris* fireflies, Barber seems to have concluded that in general *Photuris*

Fig. 1. Female of *Photuris* "C" eating a *Photinus macdermotti* male she has just attracted by mimicking the sexual signal of a *P. macdermotti* female. She has "peeled" up her prey's wings to reach the abdomen, a technique not previously observed. Site near Waldo, FL.

females are predaceous: ". . . for the female *Photuris* eats other fireflies" (p. 5; see also McDermott 1958: 9). Barber was the first to ask specifically whether signal deception was the tactic being used by the predators: "Sometimes the familiar flashes of a small species of *Photinus* . . . are observed excitedly courting a female, supposedly of the same species, whose response flashes appear normal to its kind, but when the electric light is thrown upon them one is startled to find the intended bride of the *Photinus* is a large and very alert female *Photuris* facing him with great interest. Does she lure him to serve as her repast?" (p. 10, 11). The question was answered when a female *P. versicolor* was observed to attract a male *Photinus macdermotti* by emitting flashes like those of *P. macdermotti* females (Lloyd 1965)—and as it later was recognized, by also mimicking the flashes of competing *P. macdermotti* males (Lloyd 1981a). The female then seized and began to eat the male. Farnworth (1973) found that in Jamaica *Photuris jamaicensis* preys upon several *Photinus* and a *Robopus* species. It was then demonstrated that individual females of *P. versicolor* have repertoires and are able to switch among the signals of different prey species (Lloyd 1975). Considerable evidence and numerous observations now indicate that aggressive mimicry is used by females of most *Photuris* species, excepting those of the *congener* group, and that a number of species, perhaps most or all, prey upon more than one species (Lloyd 1978, 1981c, 1983). Some *Photuris,* perhaps all that are predaceous, under certain circumstances attack flying, luminescing fireflies, guided by their targets' lights, and some use this tactic in conjunction with aggressive mimicry

(Lloyd 1983, 1984a; Lloyd and Wing 1983).

Aggressive mimicry by *Photuris* is probably one of the more important selection pressures affecting firefly signaling behavior in the Western Hemisphere (Lloyd 1981c, 1983, 1984a; Cicero 1984). Because of the intense mate competition among male fireflies and strongly male-biased, operational-sex-ratios (Lloyd 1979a), males would seem to be an "eager" and abundant prey, but this may be illusory, for prey fireflies have certainly evolved various and complex counter-measures against aggressive mimicry (Lloyd 1965, 1983, 1984a,b). In a study in which individual (n=199) *Photinus collustrans* were followed for a total of nearly 11 measured miles, they were answered 5.5 times more often by *Photuris* than by their own females (11 vs 2), but no male was captured or closely approached a hunter, though the 2 conspecific females were quickly approached and mated (Lloyd 1979a). The mode of hunting of these predators has also been a major influence on the signaling behavior of their own males, and apparently is the reason that males of several *Photuris* species emit flash patterns that are similar or identical to those of males of species that occur with them. In most cases this is probably a mate-seeking tactic, with males mimicking their females' prey to locate potential mates (Lloyd 1980), but in some it is possibly a counter-measure against their own *Photuris* predators (Lloyd in prep. and prog.; see Lloyd 1983 and below).

Evidence Levels

Conclusive evidence for the aggressive mimicry of any *Photuris* species is the observation of the entire mimicry-attraction-ingestion sequence. The firefly must be observed to emit a luminescence that resembles with "some degree" of refinement (deliberately ambiguous because the "degree" depends upon the refinement of the particular dupe's signal processing system, see Lloyd 1984a), emissions of known attractive value to the dupe—e.g. emissions of potential mates, or of conspecific males near available females. Because females of many *Photuris* species are known to be aggressive mimics, less than complete evidence for the aggressive mimicry of females of other *Photuris* species may be strongly indicative or virtually conclusive. I have arranged the evidence I have accumulated over the past 20 years according to a hierarchy of *Evidence Levels* ranging from 1 to 12 (Table 1). For "completeness," in the table I have interposed "logical" levels not observed, as well as a 0 (zero) level for fireflies that belong to a class not known to have any representatives that are observed aggressive mimics (i.e. fireflies other than *Photuris* females), but that reveal "suspicious" behavior. For example, *Photuris* males have eaten fireflies they have been confined with (McDermott 1910, pers. obs.); have been observed to answer the flashes of *Photinus* males and penlight simulations with flashes like those of *Photinus* females; and in one case, to attract a *macdemotti* male from 3 m to 10 cm. But since no male has been observed to completely attract and then eat a male of another species, these observations must be considered "suspicious." Likewise, *Photuris* larvae have been seen answering *Photinus collustrans* males, in a manner very much like that of *P. collustrans* females, and the males approached closely (T. Forrest, U. of FL, pers. comm.; see also Sivinski 1981).

Observations and Records of Occurrence

My observations began in 1963, and, with respect to taxonomic representation, were usually incidental to other field work. The lists of mimics and prey would otherwise certainly be much longer and include many more observations at Level 12. To make this summary 2716 pages of field notes of work within *Photuris*' range, and about 50 magnetic tapes of electronic flashes with associated notes were examined. Previously published estimates of totals (e.g. Lloyd 1975, 1978, 1979a, 1980, 1983) were generally correct with respect to actual predations observed (Table 1, level 12), but greatly underestimated the accumulated other evidence. The recognition that certain predator species, presumed to be sibling species on the basis of distinct male flash patterns, were but single species with more than one distinct male pattern, resulted in a reduced estimate after 1978.

These data can be used only with caution to answer questions about the importance or relative representation of various prey in the dietary budget

TABLE 1. Evidence levels for firefly aggressive mimicry.

0. A luminescent firefly, not a *Photuris* female, flashes an answer to a male firefly in the field, or an artificial pattern in the field, in a manner and form resembling that of the mating or mating-associated flashes or glows common to the answered species or species simulated.
1. A *Photuris* female eats another firefly when confined with it in a cage.
2. A *Photuris* female is found eating a male firefly in the field, or chemical analysis of a female reveals the presence of compounds occurring in other fireflies but not in *Photuris*.
3. A *Photuris* female flash-responds to an artificial pattern in the field in a manner resembling that of the mating or mating-associated flashes or glows common to a simulated, sympatric species.
4. A *Photuris* female flash responds to the flash pattern of another species in the field, in a manner resembling that of the mating or mating-associated flashes or glows of his species.
5. A *Photuris* female flash responds to the flash pattern of a male in the field, he flies closer, perhaps lands near the female.
6. Observation (3), (4), or (5) combined with (1) for the same *Photuris* female [species].
7. Observation of (3) and (2) combined for the same *Photuris* female [species] and prey species.
8. Observation of (4) and (2) combined for the same *Photuris* female [species] and prey species.
9. Observation of (5) and (2) combined for the same *Photuris* female [species] and prey species.
10. Observation of (3) with the *Photuris* female then flying to and even landing on the simulating light, the hand or mechanical parts holding it.
11. Observation of (4) with the female then flying to and hovering or darting or landing near the flashing male.
12. A *Photuris* female flashes in response to the flash pattern of a male in a manner like that of the mating or mating-associated flashes or glows common to his species and (a) he pauses in flight or approaches or lands near her, and she attacks him in the air or on the substrate by moving toward him and eats him; or (b) she remains stationary and by continuing to answer his patterns, attracts him to her, seizes and eats him.

of a particular predator because records are strongly biased by work concentration at a few sites. Regarding predation on *Photuris congener*, I only presume that Level 4, requiring a knowledge of the prey's code in order to be legitimately applied, has been fulfilled, since the flash code of *P. congener* is not understood. Males are often attracted to "erratic" flashes emitted by predators, presumably either confusing them with the flashes of their own females, or with the flashes males emit when near an available female. They were also attracted to the "erratic" flashing of a *congener* male being held and eaten by a wolf spider (Lloyd 1975).

Abbreviations for U.S. prey species in the following summaries, for *Photinus* are: ard *ardens*, col *collustrans*, con *consimilis*, csg *consanguineus*, cur *curtatus*, dim *dimissus*, fla *floridanus*, grn *greeni*, lin *lineellus*, mac *macdermotti*, mar *marginellus*, pun *punctulatus*, pyr *pyralis*, sab *sabulosus*, sci *scintillans*, tan *tanytoxus*, umb *umbratus*. For *Pyractomena* are: ang *angulata*, bor *borealis*, lnr *linearis*, luc *lucifera*. For *Photuris* are: cng *congener*, div *divisa*, undescribed species A, B, and D. Example notation: csg 3(7+) means that more than 7 females of the *Photuris* indicated, showed Level 3 evidence for their use of aggressive mimicry against *Photinus consanguineus* males.

Photuris designated by letters are unnamed species that have been under investigation for several years and that will be formally named in revisionary work in progress. Species designated by number I believe to be specifically distinct but do not know their formal nomenclatural status.

Photuris versicolor (e U.S., esp FLA): col 2(1) 3(2) 4(11) 5(4), csg 3(2) 4(1), fla 3(1) 12(1), grn 3(1), mac 3(9) 4(7) 5(6) 7(1) 10(7) 12(3), mar 5(10+), tan 2(5) 3(1) 4(5) 5(1) 12(4), "A" 1(15) 2(2) 3(6) 4(11) 5(7) 6(2) 12(5), "B" 4(1), "D" 5(2), cng 1(21) 2(5) 3(1) 4(8) 5(4) 7(12) 12(4). *Photuris cinctipennis* (FLA): csg 3(3), fla 3(1), grn 5(1). *Photuris hebes* (NY): crt 2(1). *Photuris lucicrescens* (MD, ILL): mac 3(1) 12(1), pyr 3(1) 10(1), sab 3(5) 12(1). *Photuris* "A" (FLA): col 4(1) 5(1), con 3(8), csg 3(1), tan 3(2) 12(1), umb 1(5) 12(1), cng 5(1). *Photuris* "AS" (GA): mar 3(8) 12(1). *Photuris* "B" (FLA): col 4(1), csg 3(2), fla 3(5), mac 3(3), tan 2(1) 3(2) 4(10) 5(2) 10(1) 12(1), umb 3(2), ang 2(1), "A" 2(5) 4(3) 5(2), cng 3(1) 4(2). *Photuris* "C" (FLA): fla 3(26+) 6(2), mac 3(37+) 5(48+) 12(1), Fig. 1. *Photuris* "D" (FLA): con 2(1), fla 2(1) 3(1), mac 3(4) 4(1) 5(1) 10(4) 11(1), tan 2(1) 3(3) 6(1) 12(1), "A" 2(3) 3(2). *Photuris* "E" (FLA): fla 3(1) 4(1) 10(1), grn 5(1). *Photuris* "GR" (FLA): col 1(1) 2(2) 3(1), lin 4(1), "A" 2(1) "B" 4(1). *Photuris* "LR" (FLA): mac 3(2) 5(1), umb 2(1) 4(1) 8(1). *Photuris* sp 4 (VA): near csg 7(1). *Photuris* sp 5 (VA): ign 3(1). *Photuris* sp 6 (NY): ign 3(1). *Photuris* sp 7 (NY): ign 3(1). *Photuris* sp 8 (ILL): pun 3(1). *Photuris* sp 9 (s MICH): lnr 2(2). *Photuris* sp 10 (n MICH): *Photuris* sp (conspecific?) 2(1).

Photuris jamaicensis (Jamaica): *Photinus commissus* 5(1). *Photuris* sp 1 (Colombia, S.A.): *Photinus* sp 5(1). *Photuris* sp 2 (Colombia, S.A.): *Photinus* sp 5(2); *Aspisoma* sp 5(1). *Photuris* sp 3 (Mexico): *Photuris* sp 5(3).

The following are personal communications from other observers, as indicated: *Photuris cinctipennis* (FLA): col 12(1). *Photuris versicolor* (FLA): col 4(19) 5(3) 12(4). *Photuris* "B" (FLA): col 4(21) 11(4),

T. G. Forrest, U. of Fla. *Photuris* D": mac 2(1) 3(5) 4(4) 10(6). *Photuris versicolor* (FLA): col 2(1) 5(1) mac 3(1), S. R. Wing, U. of Fla. *Photuris* "Texas Red" (TEX): dimissus 2(2+) 4(2+), J. M. Cicero, San Antonio, TX. *Photuris* sp.? (CONN): *Photinus* sp.? 12(1), G. S. Tucker, U. of Miami, Fla. *Photuris* "A"? (FLA): col 5(4). *Photuris versicolor* (FLA): lin 2(1). *Photuris* sp.? (FLA): *Deilelater atlanticus* (luminescent Elateridae; FLA) 5(1), W. Prince, Baxley, GA. *Photuris jamaicensis* (Jamaica): *Photinus commisus* 1(1), T. J. Walker, U. of Fla. *Photuris* "BR"? (FLA): col 2(1). *Photuris* "A"? (FLA): con 5(2). *Photuris* spp. (FLA): cng 3(1) 4(1) 5(1) 12(1), col 2(1), 12(1), luc 5(1), L. L. Buschman, Kansas St. U.

The following are records from the literature: *Photuris jamaicensis* (Jamaica): *Photinus commissus* 5(1), *Photinus evanescens* 2(1+) 12(1), *Photinus leucopyge* 12(1), *Photinus melanopyge* 2(1+) 12(1), *Photinus melanurus* 2(1+) 12(1), *Photinus rapidus* 2(1+) 5(3) 12(2), *Robopus montanus* 2(1+) 12(1) (Farnworth 1973); *Photinus pallens* 4?(1) (McDermott and Buck 1959). *Photuris fairchildi* (Nova Scotia): ard 5(1), bor 2(1+) 3(1+) 7(1); lnr 2(1+) 3(1+) 12(1) (Buschman 1974). *Photuris versicolor* ? (NY, MASS): ign (?) 2(1+), mar 2(1+), sab(?) 2(1+) (Hess 1917); mar 1(1+) 2(6+) (Williams 1920). See also Lloyd 1973, Table 3; 1979a; 1979b, Fig. 9; 1980; 1981b; 1981c, Fig. 1, 2, 6, 8-10, 11b, c, e*.

In summary, females of 10 *Photuris* species have been observed to attract prey males by the mimicry of the mating signals of the preys' own females, and then eat them. A conservative estimate of the total number of species that hunt by aggressive mimicry would include Levels 7-12 (Table 1) and total 12 species but a realistic estimate, taking into consideration observations of Levels 3-12 as well as comparative inference, would total 21+ species. A species that had abandoned aggressive mimicry for scavanging might eat a cage-mate (Level 1), and one that hawked its prey but did not use false signals, or that waited darkly in ambush by prey-species' females (Wing 1982), might be found eating another firefly in the field (Level 2). Females that are found eating conspecific males are another matter (see discussion, and Lloyd 1980). Ten *Photuris* are known to prey on 2 or more species; *P. versicolor* preys on 11, *Photuris* "B" on 8, and *Photuris* "A" on 6. In Florida one prey species has 6 known predators (Table 2).

Discussion

It appears that females of most *Photuris* species are aggressive mimics, and probably most or all prey on more than one species. It is now the exceptions to these generalizations that hold special interest (Lloyd 1983). Females of the *Photuris congener* group (*frontalis, divisa,* and *brunnipennis* in the U.S., and others in Latin America) comprise one set of exceptions. Species in this group are unlike other *Photuris* in a number of morphological and behavioral respects, and are commonly identified as *Photinus* in collections. Their male genitalia, important taxonomic features in the Lampyridae, are nearly identical to those of "*pennsylvanica-versicolor*-group" *Photuris*. Whether the absence of aggressive mimicry in the *congener*

*Fig. numbers refer to English manuscript of article published in Japanese.

TABLE 2. MAXIMUM EVIDENCE LEVELS (TABLE 1) OBSERVED FOR PREDATION BY *Photuris* ON SEVERAL PREY SPECIES IN NORTH-CENTRAL FLORIDA. NOTE THAT 2 PREY HAVE 6 KNOWN PREDATORS, AN IMPORTANT CONSIDERATION WHEN ANALYZING PREY SIGNALS AND COUNTERMEASURES TO PREDATORS.

		Predator Species									
		versi	cinct	A	B	C	D	E	GR	LR	BR
Prey Species	col	12	12	5	11				3		2
	con			5			2				
	csg	4	3	3	3						
	fla	12	3		3	6	3	10			
	grn	3	5					5			
	lin	2							4		
	mac	12			3	12	11			5	
	tan	12		12	12		12				
	umb			12	3					8	
	cng	12		5	4						
	A	12			5		3		2		
	B	4							4		

group is derivative or primitive will remain unknown until other Photurinae are studied.

Other *Photuris* (in the *pennsylvanica-versicolor*-group) may be idiosyncratic, and have abandoned aggressive mimicry for ecological reasons such as the absence of prey fireflies in a specialized habitat (Lloyd 1983), risk from specific predators including females of larger *Photuris*, or the adoption of alternative prey. Though prey fireflies may have valuable defensive compounds for *Photuris* (Eisner 1982), females of a Mexican species eat beetles, mosquitoes, and crane flies that they capture on grass seed-heads: Both prey and *Photuris* feed on the sticky seed coating (Lloyd 1981c, Fig. 2).

My observations lead me to suspect that many or most individual females, possibly excepting those of *P. versicolor*, are not successful in their hunting during most years and at most sites. *Photuris* populations are often much larger than those of contemporaneous, syntopic *Photinus* and *Pyractomena*, and observed capture rates are low (Lloyd 1975). Probably the material that *Photuris* females acquire as larvae permits them to produce some eggs but prey from aggressive mimicry greatly augments production. When prey is scarce or absent, mates and other conspecific males may be cannibalized by females. Toward the end of their season, when females of high reproductive value (i.e. virgins) become scarce, then absent altogether; and males age, hence their probability of future searching and finding additional mates diminishes significantly, then males may barter their bodies for a final insemination (Lloyd 1980, see Buskirk et al. 1984). How this might be accomplished is of interest. Being caught and eaten, though promoting material benefits, could indicate an unadaptive genetic predisposition, and under certain circumstances be a "poor recommendation" for a sire (Lloyd 1979a). As J. Sivinski pointed out (pers. comm.), this presumes that females have less perfect knowledge of their environment than do males: In this

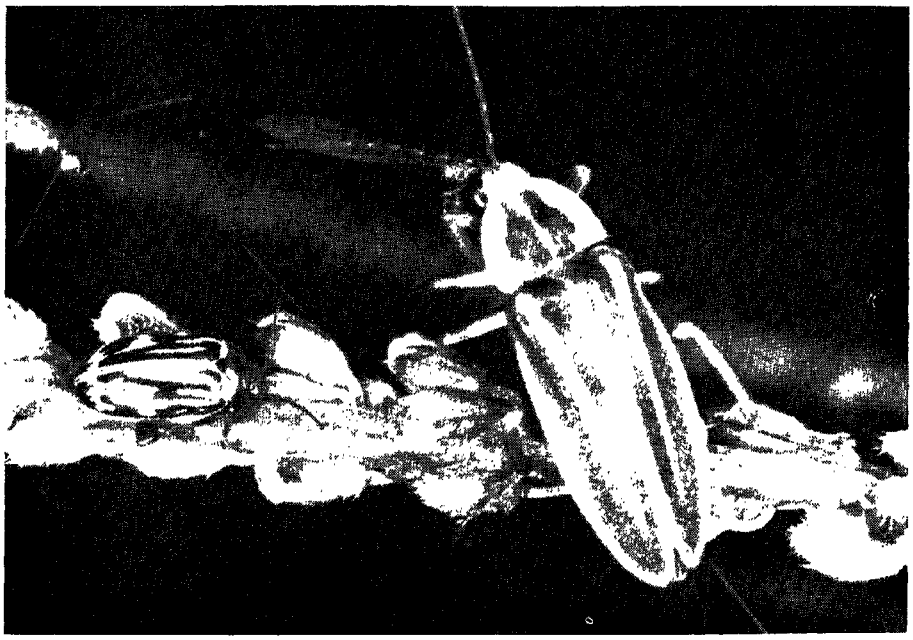

Fig. 2. Female of a Mexican *Photuris* (text sp. 3) eating a mosquito she has captured as it fed on the sticky exudate of seed-head of the grass (*Paspalum virgatum*). This *Photuris* also ate crane flies, and beetles like that in the photo. Site near Cardenas, Tabasco.

circumstance, I think that this is a reasonable possibility. In addition to questions about *Photuris* nutritional and prey budgets and economics, mating tactics and evolution, these observations on aggressive mimicry suggest questions on animal communication and deception, the significance of deception in the evolution of signals and signaling complexity, and on the use of animal signals for taxonomy (see Lloyd 1983, p. 151; 1984a, and in prep. and prog.).

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