genetic basis of discrimination, which might allow sister-sister discrimination.

The locations of the cues used in discrimination are not known. Egg-stage switches indicated that eggs or the comb, or their combination, are adequate for discrimination of a sister's comb from a nonsister's. For several reasons (*7*) we suspect that discrimination cues reside in the comb, not in brood members themselves, and are odors applied by the foundress (*8*). If foundresses do odor-mark combs, then brood discrimination may be based on the same cues as those used by *Polistes* females in adult kin recognition (*9*).

The reproductive status of preworker brood depends largely on their order of eclosion. Early emergents are workers, whereas later females are more likely to be potential queens (males do not appear until later in the summer). For this reason, age-biased responses to foreign brood could be expected and, in fact, such a bias appeared (Table 1); eggs were more often destroyed than were younger larvae, and older larvae and pupae were seldom destroyed. Also, the proportion of brood destroyed increased in older combs for both nonsister and sister switches (*10*). Desertions were uncommon in later nonsister switches as compared to NS-E switches (Fig. 1); only one NS-L and one NS-P female deserted (neither female was relocated).

Response to foreign brood on the basis of relatedness might be important for *Polistes* females in at least two natural contexts: (i) cooperative colony-founding associations of sisters (*11*) and (ii) usurpation of a single foundress's comb by another female (*12, 13*), usually one of unknown origin (*13*). Subordinate foundresses in associations tolerate their dominant sisters' brood and thereby probably increase their own inclusive fitness. In contrast, usurpers show age-specific brood destruction patterns very similar to those observed in our nonsister experimental switches (*13*). Older brood are spared and are later, as workers, exploited by the usurper to rear her own offspring. By destroying brood the usurper gains three probable advantages: (i) cells are emptied for her own eggs, (ii) she removes a competitor's genes, and (iii) brood eaten by herself or fed to older larvae are a valuable food resource.

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4. Nests were matched as closely as possible for comb size, position in the nest box, and brood composition. A 20-minute interval passed between removal and replacement of nest boxes. An empty nest box was placed within 5 to 10 m of each switched nest box. We observed foundresses for an hour after their return and mapped the brood in the combs before switches and after observation. We also mapped brood and counted adults at 2-day intervals in all study colonies from nest initiation until emergence of the first workers or loss of the queen or comb.
5. The exceptions included three SS-P colonies that had two foundresses each and a pair of SS-P colonies, used in SS-E switches, whose queens had been later replaced by sisters. There is no evidence that these substitutions affected the experimental results.
6. Two of the deserting females joined nearby sisters and two started new combs in adjacent empty nest boxes. The other eight were not seen again.
7. Egg-eating tended to follow an all-or-none pattern in switch combs, suggesting that the comb and brood are assessed as a unit; the larvae and pupae of ants and bees are easily transferred between colonies and sometimes between species (*2*). Honey bee workers, however, discriminate between haploid and diploid drone larvae on the basis of site-independent cues [J. Woyte, *J. Apic. Res.* **4**, 65 (1965)].
8. Behaviors that may involve comb-marking include mixing saliva with wood fibers used in comb construction and rubbing the abdominal venter over the comb and its pedicel [G. J. Gamboa and H. E. Dew, *Insectes Soc.* **28**, 13 (1981); D. C. Post and R. L. Jeanne, *J. Kans. Entomol. Soc.* **54**, 599 (1981)].
9. N. Ross and G. J. Gamboa, *Behav. Ecol. Sociobiol.* **9**, 163 (1981); J. Shellman and G. J. Gamboa, *ibid.* **11**, 51 (1982).
10. Comparison of NS-E egg destruction with that in later stages may be inappropriate because some NS-E females deserted new combs before contacting all of the brood in them.
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Male Firefly Mimicry

In a report of mimicry by male *Photuris* fireflies, Lloyd presents "a complex of behavioral mimicries that is without known parallel in the animal kingdom" (*1*). Lloyd previously suggested that some *Photuris* females are aggressive mimics, mimicking the female flash of a foreign species in order to attract the foreign males as food (*2*). Here, he proposes that *Photuris* males mimic foreign male flash patterns in order to attract *Photuris* females for mating. Although Lloyd's excellent observations could be interpreted as mimicry, other mechanisms may be involved.

Lloyd's interpretation of mimicry is based on a correlational study, the apparent similarity between male *Photuris* flashes and the male courtship flashes of other firefly species. Lloyd noted similarities in flash patterns produced by *Photuris*, *Photinus*, and *Pyractomena* males, but most of his examples include flickers, glows, and single flashes, which are fairly widespread types of luminescence often seen in various firefly species. Such similarities may be incidental.

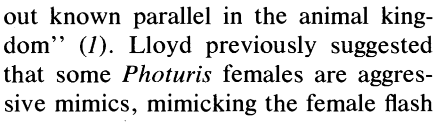

Fig. 1. Twinkles (small peaks) and crescendo flashes (large peaks) from a *Photuris lucicrescens* male during courtship. Scale bar, 2 seconds.

Mimicry by *Photuris* males would seem not to be a reproductive strategy because any male adopting this pattern will be eaten by the predatory aggressive mimic *Photuris* female that responds (something that actually occurs whenever *Photuris* males are placed in a container with *Photuris* females whether or not flashing occurs). Lloyd avoids this difficulty by assuming that male mimicry permits a male to "locate a hunting female with marginal valence for hunting and change her to a mating condition (seduction-mimicry)" (*1, 3*), but he provides no evidence that this happens. Observations on *Photuris versicolor* argue against this hypothesis (*4*). In this species only mated females adopt the behaviors (photic, locomotory, and postural) of the aggressive mimic. Virgin females do not become aggressive mimics. After mating, a behavioral switch to predation takes place. There are, apparently, no reports of aggressive mimics mating with males, and I have never observed aggressive mimics switching back to virgin answering behavior. Hence, a *P. versicolor* male that adopts the reproductive strategy of simulating the mating signal of the male of another species risks destruction, for only a predatory *Photuris* female will be attracted to such signal, not a reproductively active female. The behavioral switch *may* be different in other *Photuris* species (*5*).

As Lloyd has indicated (*6*), not all photic emissions produced by fireflies have a role in courtship or predatory behavior. Even female *P. versicolor* aggressive mimics may produce uncoordinated flashes as they fly or walk through the underbrush (*4, 7*). Hence, not all flashes made by a firefly have a role in mating communication.

In most *Photuris* species courtships have not yet been described. Thus, the exact structure of the courtship flash pattern between male and female *Photuris* fireflies is generally unknown, making it not possible to determine whether mimicry has taken place (*1*). For example, observations of *Photuris lucicrescens* courtship reveal that twinkles of 1-Hz frequency emitted by both males and females are an integral part of the flash courtship (*8*). Twinkles from the female initiate male crescendo flashing, which in turn induces female answers (Fig. 1). If one did not know the courtship behavior of this species, one might have interpreted the twinkles or crescendo flashing as examples of male mimicry.

Although females of several *Photuris* species appear to be predatory (*2*), the females of only three species of *Photuris* firefly have been reported to act like aggressive mimics (*2, 4, 9, 10*). Since male mimicry is dependent on the occurrence of female mimicry (*11*), it would seem premature to speculate about male mimicry as a general phenomenon. For male mimicry to work in a particular species, it would have to be demonstrated that (i) female mimicry exists: the occurrence of male mimicry is dependent on the occurrence of female mimicry (*11*); (ii) a behavioral switch (as in *Photuris versicolor*) is absent or, if such a switch is present, that it is reversible; and (iii) that females respond to, attract, and mate with "mimicking" males. Thus, I think that more extensive analysis is necessary, comparing the behavior of virgin and mated female fireflies, before the hypothesis of male mimicry can be accepted.

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5. Although male resource contribution might make "ultimate" sense of male mimicry as mating strategy [reference 15 in (*1*)], whether or not it actually occurs is not proved. Lloyd's account of the phenomena does not specify an instance in which a *Photuris* female found and ate (or mated with) a mimicking male, nor one where a *Photuris* male attracted or evoked answers from the female of a foreign species.
6. J. E. Lloyd, *Entomol. News* **79**, 265 (1968); *Fla. Entomol.* **52**, 29 (1969).
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11. Lloyd (*1*) appears to reject the possibility that male mimicry may have arisen in response to predation (Batesian mimicry, with *Photinus* fireflies serving as a model). For male mimicry and female mimicry to have arisen separately would make the whole mimicry story several orders of magnitude more complex.

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In reply to Copeland's comments, I offer three points for consideration.

First, in nature male fireflies emit species-typical flash patterns as they fly in their species' habitat, season, time, and space. They go to perched, answering females (*2*). This behavior cannot be observed in confined fireflies, such as the mating fireflies observed by the Copeland group (*3*). Aggressive mimicry has been observed in at least ten species (*4, 5*), and partial observations implicate several others (*6*). It probably occurs in most *Photuris* except for one small species group (*4*). In Maryland, near the source of Copeland's *lucicrescens* (*3*), I have observed this species capturing *Photinus macdermotti* and *P. sabulosus* by aggressive mimicry. It cannot be observed in the laboratory. Copeland's hesitation in applying the term "aggressive mimicry" suggests that he has not seen it in any species.

Second, the data leading to a male mimicry hypothesis include behavioral and ecological correspondences between models and mimics. Flash pattern matchings were based on extensive photomultiplier recordings of flying individuals in their habitat, and involved flash number, timing, and form [figure 1 and table 1 in (*7*)]. Mimics fly in time and space with their models (*7*, also see *Science* cover; *8*). Copeland ignores these data and matches.

Third, obviously "other mechanisms may be involved," but Copeland does not offer any that addresses the facts. I discussed six general categories of explanations for male mimicry and favored one promoting mate-finding because male mimicry occurs during a time of intense mate competition (*9*). An aggressive mimicry connection, with males searching for mated, hunting females is the best lead so far because several of their models are known prey of their females. As to how mimics get their sperm into hunters, I suggested four possibilities, including forced insemination, female selection of male phenotype, and paternal investment. I specifically restricted nuptial cannibalism to "old males with low probability for survival to the next evening's mating flight." A recent analysis augments this (*10*).

Copeland (*1*) places confidence in the value of captive behavior for revealing natural behavior. For example, *lucicrescens* emits short, explosive treetop flashes as well as crescendo flashes (*11, 12*), a point not noted by Copeland *et al.* (*3*). The short, "treetop" flash is the counterpart of and may even be mimicry, and it is used in mating in Kansan *lucicrescens* (*12*). Copeland could not see the relevant pattern and behavior in captives. The behavior of females is also influenced by captivity. When confined in bottles, *Photuris* females often retain their eggs several days, then release them all at once and die with their tails stuck in the pile. Under other conditions they lay a few eggs at a time over 2 to 3 weeks (*13*). Egg numbers in field captures range broadly, suggesting progressive maturation and oviposition (*13, 14*). It is probable that mating is also influenced by captivity, and that mated females, if free to move about, hunt, and oviposit freely, will mate again. Mimicry by competitive, female-hunting males during prime time is better evidence for multiple mating of females than "irreversible switches", observed in (egg-bound) captives, are against it.

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