

Female preference for male courtship flashes in *Photinus ignitus* fireflies

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In *Photinus* fireflies, males produce spontaneous bioluminescent courtship flashes. Females preferentially respond to particular male flashes with flashes of their own. This study explored variation in female flash responsiveness as a function of male flash duration, female condition, lantern size, and lantern distance, as well as the relationship between male characteristics and spermatophore mass in *Photinus ignitus* fireflies. We determined female preference by scoring female flash response to simulated male flashes and determined variation in overall female flash responsiveness for laboratory-mated, laboratory-fed, and control *P. ignitus* females. Flash duration, lantern size, and body mass were recorded for field-collected males. Males were then mated to determine spermatophore mass. Females exhibited greater preference for artificial flashes representing the upper range of conspecific male flash duration and lantern size as well as flashes produced at a closer distance. Both laboratory-mated and laboratory-fed *P. ignitus* females showed lower overall responsiveness across all flash durations relative to control females that did not mate or feed in the laboratory. Male flash duration predicted a significant proportion of the variation in spermatophore mass for early-season males. These results suggest that female *Photinus ignitus* may prefer long flashes in order to obtain the direct benefit of larger spermatophores and may adjust their overall flash responsiveness as the relative importance of this benefit varies with changing female condition. *Key words*: fireflies, lampyrids, mate choice, nuptial gifts, *Photinus*, sexual selection, spermatophore. [*Behav Ecol* 14:135–140 (2003)]

Female choice for particular male courtship traits has been demonstrated in many species (Andersson, 1994; Johnstone, 1995) and has been proposed to play a role in the evolution of elaborate male traits (Darwin, 1871) and speciation (Endler, 1989; Lande, 1981; Ryan, 1990). Mate choice is the pattern of mating that arises at least in part through the mating preferences of one sex (Heisler et al., 1987). As potentially adaptive behaviors, female mating preferences are predicted to vary in response to many factors, including the female's ability to discriminate between different signals and the relative costs of sampling multiple males (Jennions and Petrie, 1997). Until recently, variation in female preference and the factors underlying this variation have received little attention (Jennions and Petrie, 1997; Widemo and Saether, 1999). To determine the potential for sexual selection through female choice, we need to explore the factors that influence female mating preference.

Nuptial gifts provided by males during courtship or mating can influence female mating preference. Under certain conditions females may benefit from choosing carefully among phenotypes of prospective mates, while under other conditions females may benefit more by obtaining a male's contribution regardless of male phenotype. In many insects females can increase their reproductive output by obtaining spermatophores through additional matings (reviewed by Boggs, 1995; Gwynne, 1997; Vahed, 1998). However, in some species, females use male traits to predict spermatophore quality (e.g., Dussourd et al., 1991). Therefore, female preferences may vary with the reliability of male traits as predictors of spermatophore quality as well as with the effects of these nuptial gifts on female condition.

We studied the relationship among female preference for male traits, male spermatophore quality, and female

condition in *Photinus* fireflies. Courtship and flash behavior have been described for several *Photinus* firefly species (Branham and Greenfield, 1996; Buck, 1937; Buck and Buck, 1972; Carlson and Copeland, 1988; Cicero, 1983; Lewis and Wang, 1991; Lloyd, 1966; Wing, 1984). Male *Photinus* fly while spontaneously flashing, and females perched in the vegetation may or may not respond to the flashes of particular males with bioluminescent flashes of their own. Males that elicit a higher female response rate are more likely than competing males to successfully mate with the responding female (Lewis and Wang, 1991; Vencl and Carlson, 1998). Females differentially respond to conspecific male flashes as a function of flash rate in a species that produces trains of multiple flash pulses (*Photinus consimilis*; Branham and Greenfield, 1996) and intensity in a single-pulse species (*Photinus pyralis*; Vencl and Carlson, 1998). In single-pulse fireflies the duration of male flashes may be an important timing component assessed by females, but this has yet to be investigated. Furthermore, the adaptive significance of female preferences remains unknown for *Photinus* fireflies.

Male fireflies of the species *Photinus ignitus* transfer a protein-rich spermatophore to females during mating (van der Reijden et al., 1997). Amino acids obtained from male spermatophores are distributed to the female's eggs within 2 days after mating (Rooney and Lewis, 1999). Because adult *Photinus* fireflies do not feed in the field (Lloyd, 1997; Williams, 1917), male spermatophores may represent the only nutritional supplementation that females receive as adults. Therefore, females are expected to show preference for any male traits correlated with large spermatophores. In contrast, under some conditions females are not expected to show mating preferences because the costs of rejecting any spermatophore contribution may outweigh the benefits of choosing a particular male.

In this study we examined the hypothesis that female *P. ignitus* fireflies respond preferentially to males based on male flash duration. We also investigated whether male flash duration, body size, or lantern size might be a useful predictor of spermatophore size. Finally, we tested the prediction that

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P. ignitus female responsiveness would decrease after mating, as the costs of sampling additional males decline relative to the benefit of receiving additional spermatophores.

MATERIALS AND METHODS

We collected *P. ignitus* fireflies throughout their mating season from late June to early August 1997–2000 at the Smith Andover field in Lincoln, Massachusetts, USA. Nightly flight periods of male *P. ignitus* last from approximately 2100 to 2200 h. Fireflies were maintained in the laboratory on a natural light cycle in clear 250-ml plastic containers with moistened filter paper.

Intraspecific variation in male flash duration

To examine intraspecific variation in flash duration, we observed male *P. ignitus* both in the field and in the laboratory. We transferred spontaneously flashing males to mesh containers and recorded flashes using a photomultiplier tube connected to a portable data acquisition system (DASport, Intelligent Instrumentation, Tucson, Arizona). Flash data were acquired at 1000 Hz and streamed to disc on an IBM Thinkpad 750. Male flashes were analyzed with Visual Designer 3.0 software (Intelligent Instrumentation). We measured flash duration as the time interval from one-half maximal intensity at the onset of each flash to one-half maximal intensity as the flash decayed. This procedure removed variation that might arise due to measurement errors in the flash waveform tails.

We measured flash durations for 31 *P. ignitus* males in 1997–1998 at temperatures ranging from 51° to 83°F. Flash duration depends on temperature, so we adjusted male flash durations to a common temperature of 75°F using the equation: duration (ms) = $-4.8(\text{temp. } ^\circ\text{F}) + 448.1$ (regression: $r^2 = .84$, $n = 31$, $p < .001$). To determine whether males showed consistent flash durations, we estimated repeatability by partitioning variation within and between males using a one-way random effects ANOVA (Boake, 1989). To eliminate any possible variation due to temperature correction, repeatability of flash duration in each species was determined only for 8 males recorded at 75°F (2–9 flashes each, 33 flashes total).

Male flash behavior, morphology, and spermatophore mass

We determined the relationship among male flash behavior, morphology, and spermatophore mass for 36 *P. ignitus* males collected from 20 June to 2 July 2000, when the sex ratio is male biased and females have the opportunity to choose among males whose spermatophore contributions have yet to be compromised by multiple matings (Cratsley, 2000). Males were weighed to the nearest 0.1 mg, videoimaged, and lantern area and maximum width were measured using NIH Image.

To determine spermatophore mass, we first allowed each male to mate with a field-collected female. We interrupted copulations shortly after spermatophore transfer and froze females to prevent spermatophore degradation. Later, we dissected the female's reproductive tract, removed spermatophores, rinsed them in dH₂O, and dried them in a dessication chamber for 24 h. Spermatophore dry mass was measured to the nearest 1 µg on a Mettler MT5 microbalance.

We examined the relationship between spermatophore mass and male flash duration, body mass, lantern width, and lantern area using forward stepwise multivariate linear regression with a retention criterion of $p < .1$. Statistical analysis was performed using SPSS.

Female preference for male flashes

We collected female *P. ignitus* during 1998 and 1999 mating seasons. Testing was conducted between 2100 and 2300 h at approximately 75°F. Simulated male flashes were created with Visual Designer and produced by light-emitting diodes (LEDs; Radio Shack T-1^{3/4} yellow) driven by the analog output channel of a DASport data acquisition system.

To test female preference, we presented each female with a series of simulated male flashes emitted at 8-s intervals, approximating the *P. ignitus* male interflash interval. Female flash response to each male flash was scored as yes or no, depending on whether the female produced a flash before the next simulated flash. In each experiment described below, we presented four flashes of each treatment in a Latin-squares randomized block design to control for presentation order. Females responded to the simulated flashes in the same manner as they responded to natural flashes.

In the first experiment, we presented each of 25 females with a series of 20 simulated male flashes, 4 flashes at each of 5 durations chosen to represent a range of observed *P. ignitus* male flash durations: 55, 63, 71, 79, and 87 ms. In the second experiment, we tested 33 females with 3 flash durations of 80, 108, and 132 ms. These treatments represent, respectively: average *P. ignitus* male flash duration, extreme (approximately 2 SD above the mean) *P. ignitus* flash duration, and a duration beyond that observed in *P. ignitus*. In these two experiments we alternated simulated flashes between two LEDs, each positioned 24 cm from the female.

The third experiment examined the effects of lantern size and distance on female response to simulated flashes. To vary lantern size, we enclosed three LEDs in 0.5-ml microcentrifuge tubes covered with black electrical tape, leaving an opening of either 2, 4, or 6 mm² to approximate the range of lantern sizes observed in male *P. ignitus* (mean \pm SD lantern area = 3.4 ± 0.7 mm², $n = 77$). We mounted these artificial firefly lanterns within simulated firefly outlines placed 10 cm apart on a black background. Twenty-seven females received flashes from the three artificial lantern sizes at distances of 12, 24, and 48 cm to represent a range of distances within the 1-m radius across which courtship dialogs occur (Lewis and Wang, 1991).

We conducted statistical analysis for each female preference experiment using the Generalized Estimating Equations (GEE) procedure of SAS software (version 6.12, SAS Institute, Cary, North Carolina) because each female response or lack of response represents a correlated binary event. GEE allowed testing for main effects (flash duration, distance, or lantern size) with presentation order effects removed. We excluded females that did not respond to any flashes from these analyses because they offered no information on choice. Duration was treated as a continuous variable for the first experiment, with five duration treatment levels. In the second experiment, we compared female responsiveness at the two shorter flash durations, 80 ms and 108 ms, to the longest duration (outside the observed range of *P. ignitus* male flash duration). In the third experiment we treated both distance from flash and lantern size as discrete variables, using the largest lantern size and the farthest distance as reference categories.

Effects of female condition on responsiveness

To test for changes in female responsiveness associated with female mating and nutritional status, we assigned field-collected *P. ignitus* females to three experimental treatments: unmanipulated, laboratory mated, and laboratory fed. For females in all treatments, age and mating history before

collection were unknown. We tested 28 *P. ignitus* females (including the females analyzed for preference across 5 flash durations) without any laboratory mating or food supplement. Ten additional females from the field were allowed to mate once in the laboratory to field-collected males 1–3 nights before testing. A third group of 10 females received sponges moistened with 0.75 ml of 1% casein and 5% glucose in water, which females ingested. We presented females in each treatment with flashes of 55, 63, 71, 79, and 87 ms duration as described above.

We measured female responsiveness as the percentage of all simulated flashes to which each female responded. We used a nonparametric Kruskal-Wallis test to compare female responsiveness across the treatments because data were not normally distributed. Pairwise comparisons of responsiveness between unmanipulated, field-collected females and laboratory-mated or laboratory-fed females were made using Dunn's technique for nonparametric multiple comparisons to a control (Zar, 1999).

RESULTS

Intraspecific variation in male flash duration

Flash durations of individual *P. ignitus* males ranged from 56 to 123 ms, with a mean (\pm SD) duration of 77.3 ± 12.8 ms (Figure 1). Ninety percent of *P. ignitus* males generated flashes between 56 and 89 ms in duration, corresponding to the range tested in the first female preference experiment. Flash duration was highly repeatable for individual *P. ignitus* males (one-way ANOVA, $R = .92$).

Male flash behavior, morphology, and spermatophore mass

Male flash duration and body mass together explained a significant proportion of the variation in spermatophore mass (Table 1). Male flash duration was the single best predictor, accounting for 20% of the variation in spermatophore mass (Figure 2). Neither male lantern width nor lantern area predicted spermatophore mass.

Female preference for male flashes

Responsiveness of individual *P. ignitus* females tested in the laboratory ranged from 15–100% when simulated male flashes varying in duration were presented to females. Mean female response increased as flash duration increased, reaching a maximum of 74% at 87 ms in *P. ignitus* (Figure 3a). After accounting for order of flash presentation (GEE; presentation order $Z = 2.14$, $p = .032$), female responsiveness significantly increased with increasing flash duration (GEE; flash duration $Z = 2.46$, $p = .014$).

In the second experiment we tested *P. ignitus* females with longer simulated flashes. Female responsiveness again increased with increasing flash duration up to 108 ms (Figure 3b). This represents the upper range of flash durations produced by *P. ignitus* males (Figure 1). However, female response declined significantly when females were presented with simulated flashes longer than those produced by conspecific males (GEE; 132 ms vs. 80 ms: $Z = 5.29$, $p < .00005$; 132 ms vs. 108 ms: $Z = 6.40$, $p < .00005$).

In the third experiment, female responsiveness increased with increasing artificial lantern area at each distance tested (Figure 4). Simulated flashes from the largest lantern elicited significantly greater female response than flashes from the smallest lantern (GEE; $n = 27$, $Z = -6.46$, $p < .0001$), but there was no significant difference in female response between largest and intermediate lanterns (GEE; $n = 27$, $Z = -1.60$,

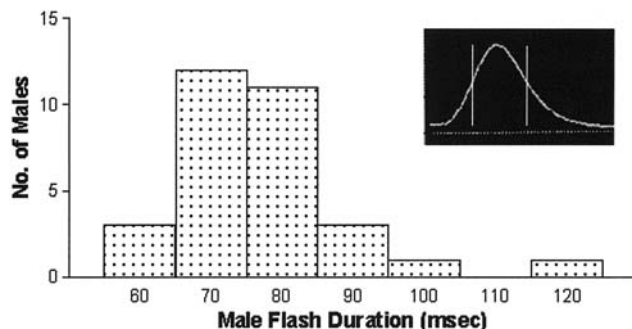


Figure 1
Variation in duration of courtship flashes for individual *Photinus ignitus* males ($n = 31$; durations averaged across 2–73 flashes per male). Flash durations measured from one-half maximal intensity at flash onset to one-half maximal intensity during flash decay, and temperature adjusted to 75°F using the equation: corrected duration = measured duration (ms) – 4.8 (75°F – measurement temperature °F).

$p = .11$). Female responsiveness decreased as the distance to the artificial lantern increased (Figure 4). The longest distance (48 cm) elicited significantly lower female response than either the shortest distance or the intermediate distance (GEE; $n = 27$, for 48 cm vs. 24 cm lantern distance, $Z = 4.27$, $p < .0001$, and for 48 cm vs. 12 cm lantern distance, $Z = 6.70$, $p < .0001$).

Effects of female condition on responsiveness

For individual, field-collected, unmanipulated *P. ignitus* females, responsiveness to 20 simulated male flashes (four flashes at each of five durations: 55, 63, 71, 79, and 87 ms) ranged from 0 to 100%, with a mean responsiveness of nearly 50% (Figure 5). Responsiveness to the same series of artificial flashes was considerably lower both for females that had recently mated and females fed a solution of casein and glucose. Female responsiveness differed significantly among these treatments (Kruskal Wallis test, $H = 6.42$, $p = .04$). Pairwise comparisons of laboratory-mated and laboratory-fed females to the field-collected control treatment indicated a significant decrease in responsiveness for laboratory-mated females and a nonsignificant decrease for fed females (one-tailed Dunn's nonparametric test, laboratory-mated females: $Q = 2.09$, $p < .05$, fed females: $Q = 1.93$, $.05 < p < .1$).

DISCUSSION

This study demonstrates that *P. ignitus* females respond preferentially to longer male flash signals. Females also showed higher response to brighter flashes but were unable to discriminate between differences in flash intensity

Table 1
Multiple regression predicting male *P. ignitus* spermatophore mass based on flash duration, body mass, lantern width, and lantern area ($n = 36$ males).

Variable	Slope (b)	p	Partial r
Spermatophore mass: $R^2 = 0.31$; $F_{2,33} = 7.33$; $p = .002$			
Flash duration (ms)	0.447	.004	.446
Body mass (mg)	0.343	.024	.343
Rejected terms			
Lantern width (mm)	-0.130	.643	-.082
Lantern area (mm ²)	-0.195	.422	-.142

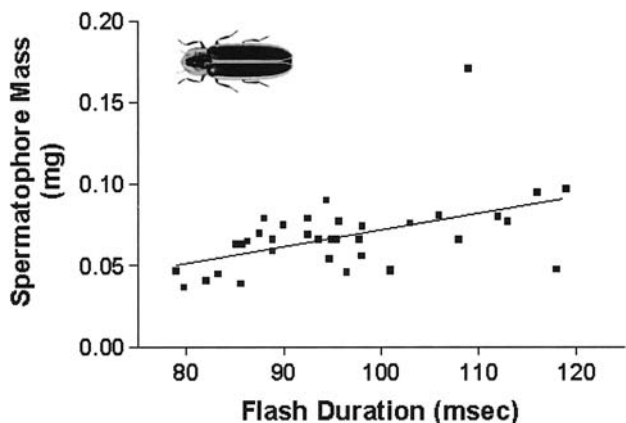


Figure 2
The relationship between *P. ignitus* male flash duration and spermatophore mass ($n = 36$ males collected from 20 June to 2 July 2000; durations averaged across 1–11 flashes per male; partial $r^2 = 0.20$, $n = 36$, $p = .002$). Flash durations temperature adjusted as in Figure 1.

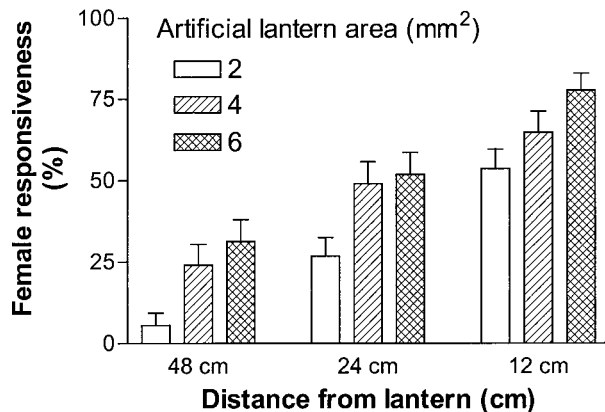


Figure 4
Mean (+ SE) percentage female response for *P. ignitus* females ($n = 27$) presented with simulated flashes from three artificial lantern sizes (2, 4, and 6 mm²) at three distances from the female (12, 24, and 48 cm).

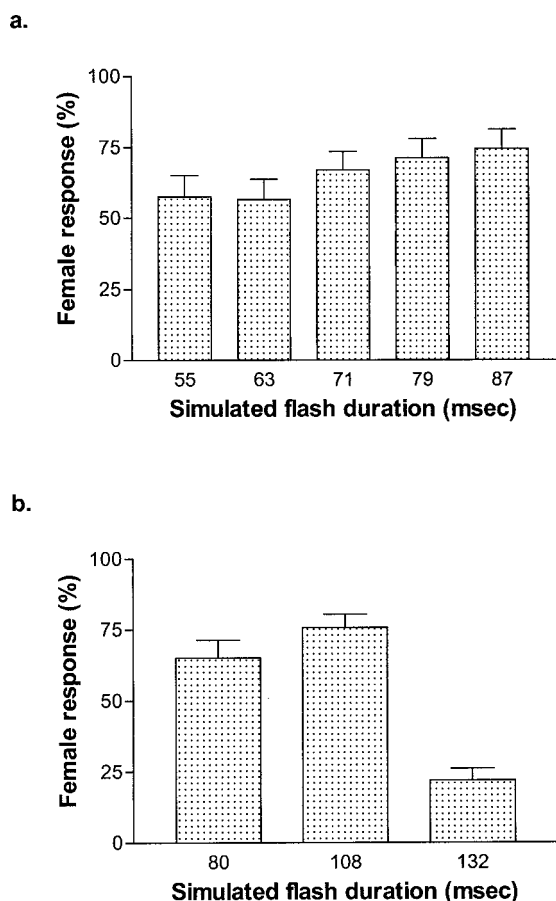


Figure 3
Mean percentage of simulated flashes (+ SE) at each duration to which female *P. ignitus* responded. Flashes were given at 8-s intervals, using a randomized Latin-squares design for presentation order. (a) Females ($n = 25$) were presented with four flashes at each of five durations representing the observed range of *P. ignitus* male flashes. (b) Females ($n = 33$) were presented with four flashes at each of three durations, representing average *P. ignitus* male flash duration, the upper limit of observed *P. ignitus* flash duration, and flash duration beyond that of *P. ignitus*.

generated by varying distance or lantern size. In addition, both male flash duration and body mass were directly related to spermatophore size early in the mating season, but male lantern size (width or area) did not contribute significantly to predicting spermatophore size. Our results also indicate that female responsiveness to male flash signals declines after females have mated or been fed. These findings suggest that female *P. ignitus* may have evolved a conditional preference for male flash duration through the direct benefits of choosing mates with the largest spermatophores.

The potential benefits of female preference have been widely debated (Andersson, 1994). On the one hand, female preferences have been theorized to result either from direct benefits (Heywood, 1989; Hoelzer, 1989; Wolf et al., 1997) or indirect genetic benefits (reviewed by Andersson, 1994; Kirkpatrick and Ryan, 1991). In contrast, female preference has also been suggested to occur in the absence of any benefit

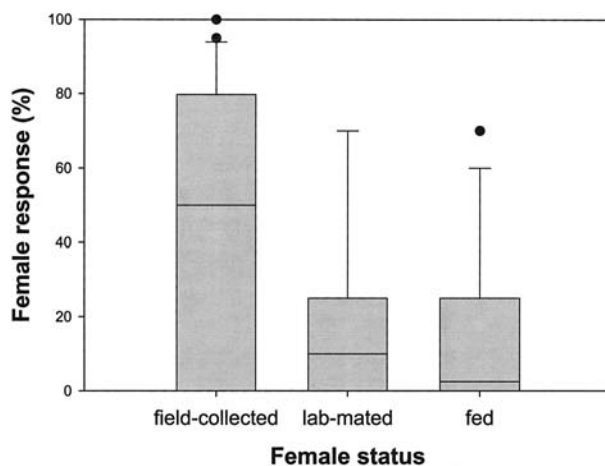


Figure 5
Percentage of 20 flashes to which *P. ignitus* females responded. Treatments were (1) field-collected females tested without further manipulation ($n = 28$), (2) females mated once in laboratory to field-collected males between 1 and 3 days before testing ($n = 10$), and (3) fed females ($n = 10$) provided with 1% casein, 5% sucrose solution for 1-5 days before testing. The box plots show the 10th, 25th, 50th, 75th, and 90th percentiles as horizontal lines and all data points outside this range.

to females, as a byproduct of existing biases in the female sensory system (Kirkpatrick and Ryan, 1991; Ryan, 1990; Ryan and Rand, 1993).

We found that female preference for long male flash duration could directly benefit females by allowing them to mate with males producing large spermatophores at least during the early part of the season. Early in the season sex ratios are male biased in *Photinus* fireflies, and female responsiveness is very low (Cratsley, 2000; Lewis and Wang, 1991). Furthermore, male spermatophore size declines significantly across successive male matings (Cratsley, 2000). Therefore, early in the season females may benefit most by mating preferentially when there is a low cost in terms of lost mating opportunities and a higher benefit from larger spermatophores. Possible alternative hypotheses for the evolution of the observed mating preference include genetic benefits and sensory bias.

Although female responsiveness increased with longer duration male flashes within the observed range of *P. ignitus*, response declined significantly when flash duration exceeded that produced by conspecific males. This finding is consistent with previous evidence that male flash duration is one aspect of flash timing that provides a mechanism to avoid courtship with heterospecifics, along with the interval between paired pulses and the number of pulses within a flash pattern (Lloyd, 1966). *P. ignitus* also co-occurs with predatory *Photuris* fireflies (Cratsley and Lewis, personal observations) that prey on male *Photinus* by mimicking female *Photinus* flash responses (Lloyd, 1965; Nelson et al., 1975; Zorn and Carlson, 1978) and by using flashes as cues to locate and attack *Photinus* fireflies (Lloyd and Wing, 1983). Therefore, reduced female responsiveness beyond the range of conspecific flash duration might serve the dual functions of species discrimination and lowered predation risk from *Photuris*.

Branham and Greenfield (1996) proposed that female preference for high flash rate in *P. consimilis* may represent an ancestral feature. However, there are fewer *Photinus* firefly species with multiple pulse flash patterns like *P. consimilis* relative to species with single-pulse flash patterns (Lloyd, 1966). This suggests that female sensitivity to male flash duration, as observed in *P. ignitus*, could be widespread in *Photinus* fireflies. In addition, female preference for larger and closer lanterns may reflect a general preference for greater flash intensity. Female *P. ignitus* responded less to all lantern sizes as distance increased, suggesting that they were assessing flash intensity rather than lantern size. Because flash intensity varies with distance, it is a potentially unreliable estimate of male phenotype.

In this study overall female responsiveness declined for mated females as well as for females fed an artificial diet, indicating that female nutritional status can influence female courtship behavior. Previous work on *Photinus* fireflies has demonstrated that female flash responsiveness in the field increases seasonally as the sex ratio becomes less male biased (Cratsley, 2000, Lewis and Wang, 1991). Rooney and Lewis (2002) also found that *P. ignitus* female fecundity increases with additional matings but not necessarily with larger spermatophore size. Because *Photinus* fireflies do not feed as adults (Lloyd, 1997; Williams, 1917), females may show increased responsiveness late in the season to secure spermatophores rather than risk missing mating opportunities.

Female nutritional status has been shown to influence mate choice for other species in which males transfer spermatophores. For instance, hungry female water mites (*Neumania papillator*; Proctor, 1991) initiate contact with a greater number of males, and hungry katydids mate more frequently (*Kawanaphile nartee*; Simmons and Bailey, 1990). Because of the widespread occurrence of nuptial gifts across many taxa,

female preferences for male traits that predict nuptial gift quality and variation in female choosiness with nutritional status may be important factors influencing the process of sexual selection in many species. Variation in female preference may occur as the cost of sampling males changes relative to the benefits of nuptial gifts, and this may provide one explanation for genetic variance in sexually selected male traits.

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REFERENCES

- Andersson M, 1994. Sexual selection. Princeton, New Jersey: Princeton University Press.
- Boake CRB, 1989. Repeatability: its role in evolutionary studies of mating behavior. *Evol Ecol* 3:173–182.
- Boggs CL, 1995. Male nuptial gifts: phenotypic consequences and evolutionary implications. In: *Insect reproduction* (Leather SR, Hardie J, eds). New York: CRC Press; 215–242.
- Branham MA, Greenfield MD, 1996. Flashing males win mate success. *Nature* 381:745–746.
- Buck JB, 1937. Studies on the firefly. II. The signal system and color vision in *Photinus pyralis*. *Phys Zool* 10:412–419.
- Buck JB, Buck E, 1972. Photic signaling in the firefly *Photinus greeni*. *Biol Bull* 142:195–205.
- Carlson AD, Copeland J, 1988. Flash competition in male *Photinus macdermotti* fireflies. *Behav Ecol Sociobiol* 22:271–276.
- Cicero JM, 1983. Lek assembly and flash synchrony in the Arizona firefly *Photinus knulli* Green (Coleoptera: Lampyridae). *Coleop Bull* 37:318–342.
- Cratsley CK, 2000. Sexual selection in *Photinus* fireflies: the roles of male courtship signals and nuptial gifts (PhD dissertation). Medford, Massachusetts: Tufts University.
- Darwin C, 1871. *The descent of man and selection in relation to sex*. London: J. Murray.
- Dussourd DE, Harvis CA, Meinwald J, Eisner T, 1991. Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). *Proc Natl Acad Sci USA* 88:9224–9227.
- Endler JA, 1989. Conceptual and other problems in speciation. In: *Speciation and its consequences* (Otte D, Endler JA, eds). Sunderland, Massachusetts: Sinauer Associates; 625–648.
- Gwynne DT, 1997. The evolution of edible ‘sperm sacs’ and other forms of courtship feeding in crickets, katydids and their kin (Orthoptera: Ensifera). In: *The evolution of mating systems in insects and arachnids* (Choe J, Crespi B, eds). Cambridge: Cambridge University Press; 110–129.
- Heisler IL, Andersson MB, Arnold ST, Boake CR, Borgia G, Hausfater B, Kirkpatrick M, Lande R, Maynard Smith J, O’Donald P, Thornhill R, Wessing FJ, 1987. The evolution of mating preferences and sexually selected traits. In: *Sexual selection: testing the alternatives* (Bradbury JW, Andersson MB, eds). New York: John Wiley & Sons; 96–118.
- Heywood JS, 1989. Sexual selection by the handicap mechanism. *Evolution* 43:1387–1397.
- Hoelzer GA, 1989. The good parent process of sexual selection. *Anim Behav* 38:1067–1068.
- Jennions MD, Petrie M, 1997. Variation in mate choice and mating preferences: a review of causes and consequences. *Biol Rev* 73: 43–78.
- Johnstone RA, 1995. Sexual selection, honest advertisement and the handicap principle: reviewing the evidence. *Biol Rev* 70:1–65.
- Kirkpatrick M, Ryan MJ, 1991. The paradox of the lek and the evolution of mating preferences. *Nature* 350:33–38.
- Lande R, 1981. Models of speciation by sexual selection of polygenic traits. *Proc Natl Acad Sci USA* 78:3721–3725.

- Lewis SM, Wang OT, 1991. Reproductive ecology of two species of *Photinus* fireflies (Coleoptera: Lampyridae). *Psyche* 98:293–307.
- Lloyd JE, 1965. Aggressive mimicry in *Photuris*: firefly femmes fatales. *Science* 149:653–654.
- Lloyd JE, 1966. Studies on the flash communication system in *Photinus* fireflies. Ann Arbor: Museum of Zoology, University of Michigan.
- Lloyd JE, 1997. Firefly mating ecology, selection and evolution. In: The evolution of mating systems in insects and arachnids (Choe JC, Crespi BJ, eds). Cambridge: Cambridge University Press; 184–192.
- Lloyd JE, Wing SR, 1983. Nocturnal aerial predation of fireflies by light-seeking fireflies. *Science* 222:634–635.
- Nelson S, Carlson AD, Copeland J, 1975. Mating-induced behavioural switch in female fireflies. *Nature* 255:628–629.
- Proctor HC, 1991. Courtship in the water mite *Neumania papillator*: males capitalize on female adaptations for predation. *Anim Behav* 42:589–598.
- Rooney J, Lewis SM, 1999. Differential allocation of male-derived nutrients in two lampyrid beetles with contrasting life-history characteristics. *Behav Ecol* 10:97–104.
- Rooney J, Lewis SM, 2002. Fitness advantage from nuptial gifts in female fireflies. *Ecol Entomol* 27:373–377.
- Ryan MJ, 1990. Sexual selection, sensory systems, and sensory exploitation. *Oxf Surv Evol Biol* 7:157–195.
- Ryan MJ, Rand SA, 1993. Species recognition and sexual selection as a unitary problem in animal communication. *Evolution* 47:647–657.
- Simmons LW, Bailey WJ, 1990. Resource influenced sex roles of zaprochilene tettigoniids (Orthoptera: Tettigoniidae). *Evolution* 44:1853–1868.
- Vahed K, 1998. The function of nuptial feeding in insects: a review of empirical studies. *Biol Rev* 73:43–78.
- van der Reijden ED, Monchamp JD, Lewis SM, 1997. The formation, transfer, and fate of spermatophores in *Photinus* fireflies (Coleoptera: Lampyridae). *Can J Zool* 75:1202–1207.
- VencI FV, Carlson AD, 1998. Proximate mechanisms of sexual selection in the firefly *Photinus pyralis* (Coleoptera: Lampyridae). *J Insect Behav* 11:191–207.
- Widemo F, Saether SA, 1999. Beauty is in the eye of the beholder: causes and consequences of variation in mating preferences. *Trends Ecol Evol* 14:26–31.
- Williams FX, 1917. Notes on the life-history of some North American Lampyridae. *J NY Entomol Soc* 25:11–33.
- Wing SR, 1984. Female monogamy and male competition in *Photinus collustrans* (Coleoptera: Lampyridae). *Psyche* 91:153–160.
- Wolf JB, Moore AJ, Brodie ED, 1997. The evolution of indicator traits for parental quality: the role of maternal and paternal effects. *Am Nat* 150:639–649.
- Zar JH, 1999. *Biostatistical analysis*. Englewood Cliffs, New Jersey: Prentice Hall.
- Zorn LP, Carlson AD, 1978. Effect of mating on response of female *Photuris* firefly. *Anim Behav* 26:843–847.