

Firefly Courtship: Behavioral and Morphological Predictors of Male Mating Success in *Photinus greeni*

Kristian Demary*, Constantinos I. Michaelidis† & Sara M. Lewis*

* Department of Biology, Tufts University, Medford, MA, USA

† Department of Biology, Swarthmore College, Swarthmore, PA, USA

Correspondence

Sara M. Lewis, Department of Biology, Tufts University, Medford, MA 02155, USA. E-mail: sara.lewis@tufts.edu

Received: June 23, 2005

Initial acceptance: August 16, 2005

Final acceptance: September 2, 2005
(S. Forbes)

doi: 10.1111/j.1439-0310.2005.01176.x

Abstract

Differences in male mating success can generate selection on male morphological traits and courtship behaviors involved in male–male competition or female mate choice. In *Photinus* fireflies (Coleoptera: Lampyridae), courtship is based on bioluminescent flash signals produced by both sexes. We conducted field observations of *Photinus greeni* fireflies engaged in competitive courtships, in which females are able to simultaneously assess several males, to identify male morphological traits and courtship behaviors that might predict male mating success. Male morphological traits did not differ between males that successfully mated compared with unsuccessful males (dialoging males that did not mate). However, courtship behavioral interactions differed: successful males tended to have higher flash pattern rates (number of flash patterns per minute), and their courtship flashes were more likely to be answered by females. We also examined how the risk of predation by *Photuris* fireflies altered courtship behavior of their *Photinus* prey. When predatory *Photuris* fireflies were present, *P. greeni* females were less likely to mate, and showed decreased flash responses to most males. However, *P. greeni* males that did successfully mate in spite of *Photuris* presence were males that maintained high flash pattern rates that elicited female responses. These results suggest that both female mate choice and *Photuris* predation exert strong selective pressures on the evolution of courtship signals in *Photinus* fireflies.

Introduction

Differences among males in their mating success constitute an important aspect of sexual selection (Darwin 1871), and many male sexual traits have been identified that enhance male competitive ability or attractiveness to females (Andersson 1994). Male-biased breeding sex ratios are expected to intensify male–male competition and simultaneously cause females to become more selective due to reduced risk of lost mating opportunities (Emlen & Oring 1977; Partridge & Endler 1987; Real 1990). When male courtship attractiveness is based on conspicuous visual or acoustic signals, predation risk can also exert a major influence on mating behaviors

and courtship signal evolution (Cade 1975; Endler 1980; Burk 1982; Ryan et al. 1982; Lloyd 1997).

Photinus fireflies are highly amenable for studies of courtship behavior because both sexes produce bioluminescent courtship signals (Lloyd 1966; Buck & Buck 1972; Carlson & Copeland 1985). The search phase of *Photinus* courtship begins near dusk, when males fly at 1–2 m elevations emitting advertisement flashes to stationary females perched near the ground. Females respond to a subset of males by producing their own flash. Many *Photinus* species exhibit a non-resource-based lek mating system in which stationary females simultaneously assess many signaling males (Cicero 1983; Vencl & Carlson 1998; Lewis & Wang 1991; Cratsley & Lewis 2005).

The dialog phase of courtship begins when a male perceives a female's response flash; the male then lands and continues dialoging as he approaches the female in short flights or by walking. Males often outnumber females early in the mating season (Lewis & Wang 1991; Cratsley & Lewis 2005), and flying males are attracted to ongoing male–female dialogs (Case 1984; Vencl & Carlson 1998). As a result, competitive courtships defined here as two or more males dialoging with a single female, are common. Although the majority of *Photinus* species studied to date have promiscuous mating systems (reviewed by Lewis et al. 2004), copulatory mate-guarding limits both sexes to a single mating per night (Lewis & Wang 1991).

Photinus courtships afford opportunities for both mate choice and mate competition (Lloyd 1979; Carlson & Copeland 1985, 1988; Vencl & Carlson 1998; Cratsley & Lewis 2005). During the search stage of courtship, *Photinus* males engage in scramble competition to elicit and perceive female responses, and females exercise choice by responding, or not, to particular males. During the dialog stage several courting males may be present, and *Photinus* females again preferentially respond to particular males, directing their flash response by aiming their abdominal lantern toward those males (Buck & Case 1986). Male scramble competition also continues throughout the dialog stage, as the first male to contact a female generally goes on to mate. Several studies have used photic playback experiments to demonstrate that females discriminate among male flash signals based on temporal variation in pulse rate or pulse duration, depending on the species (Carlson et al. 1976; Buck & Case 1986; Branham & Greenfield 1996; Cratsley & Lewis 2003; own data). In addition, field observations of *Photinus* courtship indicate that in competitive courtships with several dialoging males, males that elicit more female flash responses are more likely to succeed in mating (Lewis & Wang 1991; Vencl & Carlson 1998; Cratsley & Lewis 2005).

Many *Photinus* firefly species are sexually dimorphic with males having larger light-producing lanterns and larger eyes than females (Lloyd 1966; Case 1984; Lewis et al. 2004). Larger male lanterns may enhance males' search ability by increasing signal transmission distances, and larger eyes may improve males' ability to locate females. However, there are conflicting results from different *Photinus* species about how male morphology affects mating success (Vencl & Carlson 1998; Cratsley & Lewis 2005).

Photuris fireflies are a major predator of *Photinus*, using the latter's courtship signals to catch signaling males in flight (Lloyd & Wing 1983), and engaging in aggressive mimicry; *Photuris* females imitate the flash responses of females from various prey species, thus luring and capturing *Photinus* males (Lloyd 1965, 1997). Although Lloyd (1997) suggested that *Photuris* predation may be a major selective force on *Photinus* signaling systems, little work has examined how these predators impact *Photinus* courtship behavior.

In this study, we examined courtship behavior and mating success of *Photinus greeni* males. We conducted field observations of *P. greeni* competitive courtships (two or more males dialoging with a single female) over two mating seasons, and measured courtship flash behaviors and male morphological traits to determine which traits were correlated with male mating success. In addition, during one season we investigated the effect of predatory *Photuris* fireflies on *Photinus* courtship interactions.

Methods

Photinus greeni Courtship Observations

Populations of *P. greeni* were observed in an open field habitat in Lincoln, MA (Smith-Andover field: 42°26'N, 71°18'W) throughout the 2000 and 2004 mating seasons. The observations reported here were conducted early in the mating season, when sex ratios were male biased (June 18 to July 3, 2000 and June 17 to June 28, 2004). *Photinus greeni* is a dusk-active species, with male advertisement flashes beginning approx. 15 min after sunset. The male flight period lasts for approx. 45 min, and most *P. greeni* dialogs have ceased by 90 min after sunset. Focal females were located at the beginning of the male flight period by their responses to males or to simulated male flashes. We recorded the number of paired flash patterns emitted by each male signaling within a 1-m radius of the focal female, as well as the number of female responses to each male. Courtships were continuously observed until pairs reached stage II (tail-to-tail) copulation, when the male spermatophore is transferred to the female (van der Reijden et al. 1997); courtships that did not end in mating were not included in this study. We then collected the mating pair and all the unsuccessful dialoging males that could be located, and brought beetles into the laboratory for morphological measurements. We categorized males according to their mating outcomes. In 2000, we collected

behavioral data from 12 successful males and 24 unsuccessful dialoging males (called unsuccessful males), and morphological data from 13 successful and nine unsuccessful males. In 2004, we collected behavioral data from eight successful males and 17 unsuccessful males, and morphological data from nine successful and 15 unsuccessful males.

Behavioral Correlates of Male Mating Success

In 2000, we recorded *P. greeni* courtship behavior using Observer 3.0 (Noldus Technologies, Noldus Information Technology, Wageningen, The Netherlands) on handheld Psion Walkabout computers (Noldus Technologies, Noldus Information Technology, Wageningen, The Netherlands). In 2004, we videotaped competitive courtships using a Sony TRV80 camcorder (Sony Electronics Inc., Oradell, NJ, USA) and used the audio-track to record male flashes and female responses. From these continuous behavior recordings in both years, we calculated 'male flash pattern rate' (number of double-pulsed flash patterns emitted by each male divided by total observation time in min). In 2004, we also measured the interpulse interval (time in seconds from start of the first pulse to start of the second pulse) in the double-pulsed flash patterns of courting males. Previous studies have shown that *P. greeni* females respond differentially based on the interpulse intervals of simulated male flash signals (Buck & Buck 1972; Buck & Case 1986; own data). We measured the interpulse intervals of courting males using frame-by-frame analysis of digitized videorecordings with iMovie 4 (Apple Computers Inc., Cupertino, CA, USA). As flash timing is temperature dependent, these measured interpulse intervals were temperature adjusted to a common temperature of 70°F (using polynomial regression, own data). We were unable to videorecord all flashes emitted by each dialoging male, and the data presented here on interpulse intervals are restricted to only those males for which we recorded greater than or equal to three flash patterns (five successful and five unsuccessful males).

In both 2000 and 2004, our continuous behavior recordings of focal females were also used to calculate two measures of each female's flash responsiveness to each male. First, we calculated 'female response', based on the percentage of a given male's flashes that elicited a female flash response. We also looked at 'female flash allocation' to each male, defined as the percentage of all the female's response flashes that were directed toward a given male. This

latter measure controlled for differences in overall responsiveness among focal females, which in *Photinus ignitus* has been shown to vary with female nutritional and mating status (Cratsley & Lewis 2003).

Morphological Correlates of Male Mating Success

In the laboratory, male mass was measured to the nearest 0.1 mg, and each male was digitally photographed. NIH ImageJ (National Institutes of Health USA, <http://rsb.info.nih.gov/ij/>) was used to measure elytral length, lantern width (maximum width measured perpendicularly to longitudinal body axis), metatibia length (measured only in 2004), and eye size (distance between the lateral edges of the compound eyes measured perpendicularly to body axis). We calculated condition index for each male as the ratio of body mass (mg) to elytral length (mm).

Statistical Analysis

We compared morphological and behavioral traits between those males that successfully mated with females in competitive courtships (successful males) and those males that dialoged with females but failed to mate (unsuccessful males). Data from each year were analyzed separately because trait distributions varied between years. We first examined differences between successful and unsuccessful males by conducting separate variance t-tests on individual traits (Systat 11, SPSS Inc., Chicago, IL, USA); this univariate approach allows males to be included even when they are missing data for other variables, and can be useful in interpreting multivariate analyses. Because many of the morphological traits were correlated with one another, we also used principal component analysis (PCA) on the morphological trait correlation matrix to concisely summarize morphological variation among males from each year; contributions made by each variable to the first two principal components were evaluated by significance tests of the correlation coefficients, taking sample sizes into account (Stevens 1986). We then used multiple logistic regression to examine whether the probability of successfully mating was influenced by male morphology, as summarized by each male's morphological principal component scores. Because courtship behavioral traits were also correlated with each other, for each year we also conducted PCA on the behavioral correlation matrix; due to small sample sizes, interpulse interval was not

included in this analysis. We similarly examined how courtship behaviors influenced the probability of mating successfully using multiple logistic regression on the behavioral PCA scores; PCA and logistic regressions were conducted using JMP 5 software, SAS Institute Inc., Cary, NC, USA. All descriptive statistics are reported as $\bar{x} \pm SE$, and all statistical tests conducted were two tailed.

Courtship Disruption by Predatory *Photuris* fireflies

During our observations of *P. greeni* courtship behavior in 2000, 9 of 45 courtship interactions (20%) were disrupted by *Photuris* predatory fireflies. We examined whether the presence of *Photuris* predators affected the likelihood of courtship interactions leading to successful mating using a Fisher's exact test of a 2×2 contingency table (StatXact 4, Cyrel Software Corp., Cambridge, MA, USA). To examine how the presence of these predators influenced male's flash pattern rates and female's response behavior, for each competitive courtship we compared these behaviors before and after a *Photuris* flash was seen within 1 m of the focal female using paired t-tests.

Results

Photinus greeni Competitive Courtships

During 2000, competitive courtships lasted 21.7 ± 4.1 min ($\bar{x} \pm SE$, $n = 23$ courtships) with 3.0 ± 0.2 males dialoging with each focal female

(range was two to four males dialoging with each female). Averaged across all dialoging males ($n = 36$), *P. greeni* males emitted 1.1 ± 0.1 double-pulsed flash patterns per minute, and females responded to $32.2 \pm 3.8\%$ of male phrases.

In 2004, competitive courtships lasted 19.4 ± 3.4 min, with 3.3 ± 0.9 males (range two to four males) dialoging with each focal female ($n = 8$). Averaged across all dialoging males ($n = 25$), *P. greeni* males emitted 1.0 ± 0.1 double-pulsed flash patterns per minute, and females responded to $38.4 \pm 4.5\%$ of male phrases.

Morphological Correlates of Male Mating Success

None of the morphological traits that were measured for *P. greeni* males, including male mass, elytral length, condition index, lantern width, eye size or metatibial length helped to predict male mating success in competitive courtships during either year (Table 1; separate variance t-tests, all $p > 0.120$).

For each year, morphological variation among males was summarized using principal component analyses (Table 2a). For courtships observed during 2000, the first two principal component axes together accounted for 90.2% of the overall variation among males in these morphological traits. Factor loadings (Table 2a) indicated that the first principal component (PC1) reflected overall body size of males (approximately equal weightings of male mass, elytral length, lantern and eye sizes). The second principal component (PC2) contrasted male

Table 1. Morphological and behavioral traits of *Photinus greeni* males involved in competitive courtships during the 2000 and 2004 mating seasons

| | 2000 | | p-value | 2004 | | p-value |
|-----------------------------|------------------|--------------------|---------|---------------------|---------------------|---------|
| | Successful males | Unsuccessful males | | Successful males | Unsuccessful males | |
| Morphological traits | $n = 13$ | $n = 9$ | | $n = 9$ | $n = 15$ | |
| Male mass (mg) | 19.8 ± 1.4 | 17.9 ± 1.5 | 0.373 | 19.7 ± 1.4 | 21.5 ± 1.4 | 0.358 |
| Elytra length (mm) | 7.61 ± 0.16 | 7.56 ± 0.24 | 0.858 | 7.42 ± 0.21 | 7.84 ± 0.14 | 0.1205 |
| Condition index (mg/mm) | 2.59 ± 0.17 | 2.36 ± 0.15 | 0.317 | 2.68 ± 0.14 | 2.72 ± 0.14 | 0.8052 |
| Lantern width (mm) | 2.35 ± 0.05 | 2.33 ± 0.07 | 0.827 | 2.50 ± 0.08 | 2.60 ± 0.06 | 0.3383 |
| Eyespan (mm) | 1.53 ± 0.03 | 1.51 ± 0.03 | 0.669 | 1.46 ± 0.03 | 1.49 ± 0.02 | 0.3805 |
| Metatibial length (mm) | – | – | – | 1.55 ± 0.07 | 1.49 ± 0.05 | 0.4999 |
| Behavioral traits | $n = 12$ | $n = 24$ | | $n = 8$ | $n = 17$ | |
| Interpulse interval (s) | – | – | | 1.51 ± 0.07 (5) | 1.58 ± 0.08 (5) | 0.5242 |
| Flash pattern rate (n/min) | 1.24 ± 0.24 | 0.96 ± 0.11 | 0.301 | 1.3 ± 0.21 | 0.9 ± 0.11 | 0.1210 |
| Female response (%) | 49.6 ± 5.6 | 23.5 ± 3.9 | 0.0004 | 52.3 ± 6.6 | 31.9 ± 5.2 | 0.0276 |
| Female flash allocation (%) | 58.6 ± 8.8 | 20.7 ± 3.9 | 0.001 | 57.3 ± 6.3 | 19.0 ± 3.6 | 0.0002 |

$\bar{x} \pm SE$ are given for males that successfully mated with focal females compared with unsuccessful males (dialoging males that did not mate). Probabilities are reported from separate variance t-tests.

Table 2: Summary of principal components analyses for *Photinus greeni* males involved in competitive courtships during the 2000 and 2004 mating seasons: (a) factor loading coefficients for male morphological traits and percentage of variation explained by the first two morphological principal components; (b) factor loading coefficients for courtship flash behaviors and percentage of variation explained by the first two behavioral principal components

| | Principal components | | | |
|-------------------------------|----------------------|-----------|----------|-----------|
| | 2000 | | 2004 | |
| | 1 | 2 | 1 | 2 |
| (a) Male morphological traits | | | | |
| Male mass (mg) | 0.5253** | -0.0794 | 0.5344** | 0.0093 |
| Lantern size (mm) | 0.5463** | -0.0708 | 0.5238** | -0.4108* |
| Body size (mm) | 0.4242* | 0.8297** | 0.4375 | 0.8515** |
| Eye size (mm) | 0.4956* | -0.5480** | 0.4986** | -0.3256 |
| Eigenvalue | 2.96 | 0.65 | 2.96 | 0.58 |
| % Variation | 74.1 | 16.1 | 74.0 | 14.4 |
| (b) Courtship flash behaviors | | | | |
| Male flash pattern rate | 0.3572* | 0.8951** | 0.5794** | -0.5668** |
| Female response (%) | 0.6278** | -0.4416** | 0.5180** | 0.8109** |
| Female flash allocation | 0.6916** | -0.0614 | 0.6293** | -0.1455 |
| Eigenvalue | 1.90 | 0.93 | 1.68 | 0.77 |
| % Variation | 63.4 | 31.0 | 56.1 | 25.8 |

Statistical significance for factor loading coefficients is indicated by * $p < 0.05$ and ** $p < 0.01$.

elytral length with eye size: males with larger PC2 values had smaller eye sizes relative to their body length. As in the univariate comparisons, there were no significant differences in morphological PCA scores between successful and unsuccessful males (Table 3a; multiple logistic regression, overall model likelihood ratio $\chi^2 = 0.330$, $df = 2$, $r^2 = 0.01$, $p = 0.848$). For courtships observed during 2004, the first two principal component axes together account

Table 3: Multiple logistic regression results for 2000 and 2004 competitive courtships modeling the probability of male mating success based on: (a) principal component scores summarizing male morphological traits; (b) principal component scores summarizing courtship flash behaviors

| Source | Likelihood ratio | | | |
|-------------------------------|------------------|---------|----------|---------|
| | 2000 | | 2004 | |
| | χ^2 | p-value | χ^2 | p-value |
| (a) Male morphological traits | | | | |
| PC 1 | 0.287 | 0.5921 | 0.006 | 0.9372 |
| PC 2 | 0.044 | 0.8346 | 0.810 | 0.3683 |
| (b) Courtship flash behaviors | | | | |
| PC 1 | 16.281 | 0.0001 | 9.188 | 0.0024 |
| PC 2 | 0.437 | 0.5085 | 0.3491 | 0.5546 |

ed for 88.4% of the overall variation among males in these morphological traits (Table 2a). Factor loadings again revealed that PC1 reflected overall male body size, while PC2 contrasted elytral length with male eye and lantern size: males with larger PC2 values had smaller lantern and eye sizes relative to their body length. Again, there were no significant differences in morphological PCA scores between successful and unsuccessful males (Table 3a; multiple logistic regression, overall model ratio $\chi^2 = 0.815$, $df = 2$, $r^2 = 0.03$, $p = 0.6654$).

Behavioral Correlates of Male Mating Success

Neither male flash pattern rate nor interpulse interval (measured only in 2004) differed significantly between successful and unsuccessful males (Table 1; t-tests, all $p > 0.12$). However, in both years successful males had significantly higher female response and female flash allocation (both measures of female flash responsiveness to particular males) compared with unsuccessful males (Table 1; all $p < 0.028$). Because male flash pattern rate (no. of double-pulsed patterns per minute), female response (%), and female flash allocation (%) were all found to be highly correlated, we used PCA in each year to summarize these behavioral interactions (Table 2b).

The first two behavioral principal components summarized 94.4% and 88.4% of courtship behavior differences in 2000 and 2004, respectively. Factor loadings for PC1 were similar between years, weighting approximately equally the three behavioral variables of male flash pattern rate, female response, and female flash allocation (Table 2b). In both years, PC2 contrasted male flash pattern rate against female response or flash allocation: males with high PC2 scores received fewer female responses relative to their flash rate than males with low PC2 scores. Multiple logistic regression analyses (Table 3b) revealed significant differences in courtship behavior between successful and unsuccessful males in both 2000 (Table 3b; overall model $\chi^2 = 16.64$, $df = 2$, $r^2 = 0.36$, $p = .0002$) and 2004 ($\chi^2 = 9.36$, $df = 2$, $r^2 = 0.36$, $p = 0.0093$). In particular, the highly significant difference between successful and unsuccessful males in behavioral PC1 indicated that successful males had higher flash pattern rates, female response, and female flash allocations (Fig. 1).

Courtship Disruption by Predatory *Photuris* Fireflies

Photinus courtships that were attended by predatory *Photuris* fireflies were significantly less likely to

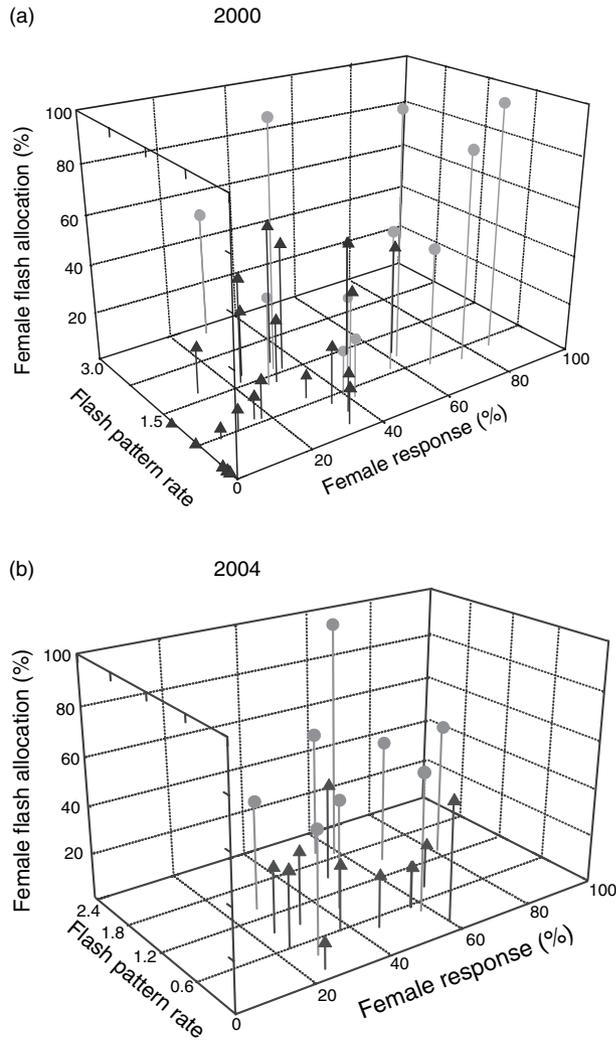


Fig. 1: Comparisons of courtship behaviors in *Photinus greeni* fireflies between successful males (circles) and unsuccessful males (triangles) in competitive courtships (greater than or equal to two males): (a) observations during 2000 mating season (12 successful, 24 unsuccessful males); (b) observations during 2004 mating season (eight successful, 11 unsuccessful males)

culminate in successful matings (Table 4; Fisher's exact test statistic = 4.48, df = 1, p = 0.05). When all courting males were considered, male flash pattern rates before *Photuris* predators arrived were higher (0.745 ± 0.154 flash patterns per minute) compared with rates after predator arrival (0.488 ± 0.133 flash patterns per minute), although this difference was not significant (paired t = 1.28, 15 df, p = 0.220). However, we observed distinct behavioral differences between successful and unsuccessful *P. greeni* males in courtships interrupted by *Photuris* (Fig. 2; because we had flash data for only

Table 4: Influence of predatory *Photuris* fireflies on the outcome of *Photinus greeni* courtship interactions

| | Focal female | | |
|-------------------------|--------------|-----------|---------|
| | Mated | Not mated | % Mated |
| <i>Photuris</i> present | 3 | 6 | 33.3 |
| <i>Photuris</i> absent | 26 | 10 | 72.2 |

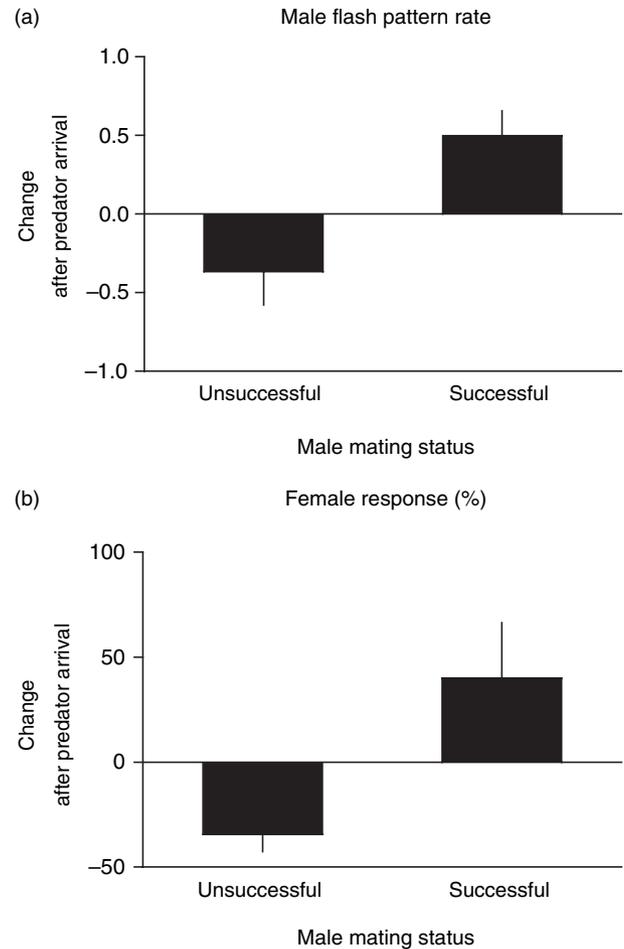


Fig. 2: Differences in *Photinus greeni* courtship behavior ($\bar{x} \pm SE$) between unsuccessful males (n = 14) and successful males (n = 2) following the appearance of a *Photuris* predatory firefly: (a) change in male flash pattern rate (each male's rate after predator arrival subtracted from rate before); (b) change in female response (the percentage of each male's flashes to which female responds after predator arrival subtracted from female response before)

two successful males, no statistical analysis was performed on these data). Those males that later went on to successfully mate showed increased flash pattern rates after predators arrived, while unsuccessful males showed lower flash pattern rates in the same situation (Fig. 2a). Similarly, overall female response

to all courting male flashes before *Photuris* predators arrived was higher ($41.9 \pm 6.5\%$) compared with rates after predators ($23.9 \pm 7.6\%$), although this difference was not significant (paired $t = 1.58$, 15 df, $p = 0.136$). However, when only males that went on to successfully mate were considered, females showed increased responsiveness to these males while they showed decreased responses to unsuccessful males (Fig. 2b).

Discussion

These observations of courtship in *P. greeni* fireflies from two mating seasons indicate that male–female behavioral interactions are the major determinants of male mating success during competitive courtships. Males that produced more flash patterns per minute that had a greater percentage of their courtship signals answered by females, and that received a higher percentage of a female's total responses were more likely to successfully mate with females (Fig. 1, Table 3). These results complement and extend studies in other *Photinus* species showing those males that elicit more female flash responses are more likely to locate and mate successfully with females (Lewis & Wang 1991; Vencl & Carlson 1998; Cratsley & Lewis 2005). However, the role of male flash pattern rate per se in determining male mating success is less clear; although in both years successful males flashed more often (Table 1), no significant difference was detected using univariate tests. In addition, it is difficult to disentangle the causal relationship between male and female flash behaviors, as males able to elicit a female response are more likely to flash again. In this study, we found no significant difference between successful and unsuccessful males in the length of time between paired pulses in the male flash pattern, although previous work on *P. greeni* fireflies has shown that the interpulse interval of simulated courtship signals affects female response (Buck & Buck 1972; Buck & Case 1986; own data). However, because of small sample sizes here, additional study is warranted concerning how male flash variation affects mating success.

In contrast to courtship behavior, differences among *P. greeni* males in body, lantern or eye size did not predict male mating success (Table 1). This finding contradicts previous evidence of morphological differences between successful and unsuccessful males in other *Photinus* species. In non-competitive courtships (single male dialoging with female) of *Photinus pyralis* fireflies, mating males had larger lanterns and elytral lengths compared with the popula-

tion \bar{x} (Vencl & Carlson 1998). This is consistent with larger male wing and lantern sizes conferring an advantage to males during the search phase of courtship. In competitive courtships, studies of different *Photinus* species have yielded differing results concerning how morphological traits affect male mating success. In *P. pyralis* competitive courtships (defined by Vencl & Carlson 1998 as greater than or equal to four males), successful males had smaller lanterns and elytral lengths compared with unsuccessful courting males. Another study (Cratsley & Lewis 2005) found that following competitive courtships (greater than or equal to two males) in *P. ignitus*, successful males had larger lanterns but elytral lengths did not differ compared with unsuccessful courting males. Some of these divergent results may reflect species differences in types and intensity of male–male competition, which may create different selective pressures. In *P. pyralis*, males engage in intense exploitative competition in which multiple males contact the female and attempt to copulate, forming 'love knots' (Maurer 1968; Vencl & Carlson 1998).

These results indicate that, beyond consumption, predatory *Photuris* fireflies may exert more subtle selection on *Photinus* courtship interactions. We found *Photinus* courtships that were attended by predatory *Photuris* fireflies were significantly less likely to culminate in successful matings (Table 4). In addition, those *P. greeni* males that did successfully mate in spite of *Photuris* presence were the males that maintained high rates of courtship signaling that elicited female responses (Fig. 2). As *Photinus* males only live approx. 2 wk and are limited to a single mating each night (Lewis & Wang 1991), lost mating opportunities are costly. Our results suggest that for at least some *Photinus* males, the cost of a lost mating opportunity may be outweighed by any predation costs incurred by more frequent courtship signals.

This study indicates that both female response to male flash signals and *Photuris* predation may represent strong selective agents in the evolution of *Photinus* courtship behavior. Future comparative studies involving different mating systems and levels of predation will provide additional insight into how mate choice, competition and predation have shaped the morphology and behavior of *Photinus* fireflies.

Acknowledgments

We thank S. Anderson for field assistance, and T. Fedina, N. Milburn, and two anonymous referees

for comments on this manuscript. Funding was provided by NSF awards IBN-9816432 and DBI-0243668, the Tufts University Faculty Research Fund, and the Swarthmore College Lande Research Fund.

Literature Cited

- Andersson, M. 1994: Sexual Selection. Princeton Univ. Press, Princeton, NJ.
- Branham, M. A. & Greenfield, M. D. 1996: Flashing males win mate success. *Nature* **381**, 745–746.
- Buck, J. E. & Buck, E. 1972: Photic signaling in the firefly *Photinus greeni*. *Biol. Bull.* **142**, 195–205.
- Buck, J. E. & Case, J. F. 1986: Flash control and female dialog repertory in the firefly *Photinus greeni*. *Biol. Bull.* **170**, 176–197.
- Burk, T. 1982: Evolutionary significance of predation on sexually signaling males. *Fla. Entomol.* **65**, 90–104.
- Cade, W. 1975: Acoustically orienting parasitoids: fly phonotaxis to cricket song. *Science* **190**, 1312–1313.
- Carlson, A. D. & Copeland, J. 1985: Communication in insects: I. Flash communication in fireflies. *Q. Rev. Biol.* **60**, 415–436.
- Carlson, A. D. & Copeland, J. 1988: Flash competition in male *Photinus macdermotti* fireflies. *Behav. Ecol. Sociobiol.* **33**, 271–276.
- Carlson, A. D., Copeland, J., Raderman, R. & Bulloch, A. 1976: Role of interflash intervals in a firefly courtship (*Photinus macdermotti*). *Anim. Behav.* **24**, 786–792.
- Case, J. F. 1984: Vision in mating behavior of fireflies. In: *Insect Communication* (Lewis, T., ed.). Academic Press, New York, NY, pp. 195–222.
- Cicero, J. M. 1983: Lek assembly and flash synchrony in the Arizona firefly *Photinus knulli* Green (Coleoptera: Lampyridae). *Coleopt. Bull.* **37**, 318–342.
- Cratsley, C. K. & Lewis, S. M. 2003: Female preference for male courtship flashes in *Photinus ignitus* fireflies. *Behav. Ecol.* **14**, 135–140.
- Cratsley, C. K. & Lewis, S. M. 2005: Seasonal variation in mate choice of *Photinus ignitus* fireflies. *Ethology* **111**, 89–100.
- Darwin, C. 1871: *The Descent of Man and Selection in Relation to Sex*. Prometheus Books, Amherst, NY.
- Emlen, S. T. & Oring, L. W. 1977: Ecology, sexual selection and the evolution of mating systems. *Science* **197**, 215–223.
- Endler, J. A. 1980: Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **43**, 76–91.
- Lewis, S. M. & Wang, O. T. 1991: Reproductive ecology of two species of *Photinus* fireflies (Coleoptera: Lampyridae). *Psyche* (Stuttgart) **98**, 293–307.
- Lewis, S. M., Cratsley, C. K. & Demary, K. 2004: Mate recognition and choice in *Photinus* fireflies. *Ann. Zool. Fenn.* **41**, 809–821.
- Lloyd, J. E. 1965: Aggressive mimicry in *Photuris*: firefly femmes fatales. *Science* **149**, 653–654.
- Lloyd, J. E. 1966: Studies on the Flash Communication System of *Photinus* Fireflies. University of Michigan, USA, Museum of Zoology, Ann Arbor, MI, USA., vol. 130, pp. 1–95.
- Lloyd, J. E. 1979: Sexual selection in luminescent beetles. In: *Sexual Selection and Reproductive Competition* (Blum, M. S. & Blum, N. A., eds). Academic Press, Inc., New York, NY, pp. 293–342.
- Lloyd, J. 1997: Firefly mating ecology, selection and evolution. In: *The Evolution of Mating Systems in Insects and Arachnids* (Choe, J. C. & Crespi, B. J., eds). Cambridge Univ. Press, Cambridge, pp. 184–192.
- Lloyd, J. E. & Wing, S. 1983: Nocturnal aerial predation of fireflies by light-seeking fireflies. *Science* **222**, 633–635.
- Maurer, U. M. 1968: Some parameters of photic signaling important to sexual and species recognition in the firefly *Photinus pyralis*. MS thesis, State Univ. New York, Stony Brook, NY.
- Partridge, L. & Endler, J. A. 1987: Life history constraints on sexual selection. In: *Sexual Selection: Testing the Alternatives* (Bradbury, J. W. & Andersson, M. B., eds). Wiley, Chichester, UK, pp. 265–277.
- Real, L. 1990: Search theory and mate choice. I. Models of single-sex discrimination. *Am. Nat.* **136**, 376–404.
- van der Reijden, E. D., Monchamp, J. D. & Lewis, S. M. 1997: The formation, transfer, and fate of spermatozoa in *Photinus* fireflies (Coleoptera: Lampyridae). *Can. J. Zool.* **75**, 1202–1207.
- Ryan, M. J., Tuttle, M. D. & Rand, A. S. 1982: Bat predation and sexual advertisement in a neotropical anuran. *Am. Nat.* **199**, 136–139.
- Stevens, J. P. 1986: *Applied Multivariate Statistics for the Social Sciences*. Harper & Row, New York, NY.
- Vencl, F. V. & Carlson, A. D. 1998: Proximate mechanisms of sexual selection in the firefly *Photinus pyralis* (Coleoptera: Lampyridae). *J. Insect Behav.* **11**, 191–207.