

## Seasonal Variation in Mate Choice of *Photinus ignitus* Fireflies

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### Abstract

Mate choice by either sex may vary with changes in the associated costs and benefits, determined by factors such as the availability of potential mates and variation in mate quality. We examined seasonal variation in operational sex ratio, courtship behavior, spermatophore mass, egg count, and the relationship between morphological traits and mating success in *Photinus ignitus* fireflies to determine if mate choice in either sex varied with the availability and relative reproductive investment of fertilizable females and sexually active males. Successfully mating males had larger lanterns than unsuccessful males when the operational sex ratio was male-biased. In addition, female responsiveness to male signals increased as the number of courting males decreased, and male spermatophore mass decreased with body size across the mating season. Successfully mating females had larger body mass than unsuccessful females. Female body mass predicted egg count and female rejection by males increased as the season progressed and female size decreased. These results suggest that both male and female *P. ignitus* exhibit mate choice, and that such choice is influenced by seasonal variation in the abundance and quality of potential mates.

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### Introduction

The operational sex ratio (OSR: the ratio of fertilizable females to sexually active males; Emlen & Oring 1977) may influence the levels of competition and choosiness exhibited by males and females during courtship behavior. OSR influences both the costs of choice because of lost mating opportunities and the importance of competition to secure mating opportunities (Parker 1983; Andersson 1994; Andersson & Iwasa 1996; Reynolds 1996). The relative costs and benefits of mate choice are also influenced by other factors such as variation in

mate quality (Owens & Thompson 1994; Johnstone et al. 1996; Jennions & Petrie 1997; Widemo & Saether 1999). Paternal investment in the form of paternal care or nuptial gifts can potentially alter the intensity of competition and choice (e.g. Gwynne 1984; Gwynne & Simmons 1990; Vincent et al. 1994) through its effect on either operational sex ratio or variation in mate quality.

Male fireflies of the genus *Photinus* transfer a nuptial gift in the form of a spermatophore to females at mating, and nutrients from the spermatophore are incorporated into the female's eggs (van der Reijden et al. 1997; Rooney & Lewis 1999). *Photinus* fireflies do not feed as adults (Williams 1917; Lloyd 1997) and spermatophores represent the only nutrient input for adult females. As spermatophores increase female fecundity (Rooney & Lewis 2002), this male investment may be an important component of mate quality. *Photinus* females may choose mates through differential responsiveness to the bioluminescent flashes produced by males (Lloyd 1979; Lewis & Wang 1991; Branham & Greenfield 1996; Vencl & Carlson 1998). Therefore, females may prefer particular flash characteristics because they are indicators of male spermatophore size (Cratsley & Lewis 2003). Additional studies indicate that *Photinus ignitus* male ability to produce a spermatophore declines over his lifespan and may constrain male mating success (Cratsley et al. 2003). Thus seasonal changes in firefly reproductive investment might be associated with changes in courtship behavior and mate choice.

We conducted this descriptive study of a natural population of *P. ignitus* to document how changes in reproductive investment and sex ratio may influence mate choice. We measured variation in courtship behavior and operational sex ratio over the course of the mating season. In addition we examined whether mating success covaried with male or female morphology in different parts of the season. Finally, we examined seasonal changes in both male and female reproductive investment in order to explore the relationship between mate quality and courtship behavior in the field.

## Methods

### Study Organism

Male *P. ignitus* fireflies fly and produce bioluminescent flashes from 21:00 to 23:00 hours each night, referred to as the male flight period. Males land after observing a female response flash and begin a courtship dialog of male flashes and female responses as the male approaches the female. Once a male locates a female he usually stops flashing, mounts the female dorsally and inserts his aedeagus into her genital opening. This is defined as stage I of mating (Lewis & Wang 1991). Stage II of mating occurs when the male swivels around 180°, but remains positioned abdomen-to-abdomen in copula with the female. During this stage of mating, the male transfers a spermatophore into the female's bursa (van der Reijden et al. 1997; Rooney & Lewis 1999). This second stage of mating can last as long as 8 h (Lewis & Wang 1991; J. A. Rooney, pers. comm.), limiting both males and females to one mating per night.

### Seasonal Patterns of Courtship and Mating Behavior

Field observations of *P. ignitus* courtship and mating behavior were conducted at Smith Andover field (Lincoln, MA, USA) throughout the mating season from June 26 to August 1, 1995. Focal females were located by their responses to simulated male flashes produced with penlights starting at approx. 21:00 hours each evening. While this may have biased our sample toward responsive females, it also insured that all females were reproductively active. The courtship dialog arena for each female was defined as a 1-m-radius circle around the female's perch site. Each female was observed for several 5-min periods, during which we recorded the number of males flashing within the dialog arena, the number of flashes from each male, and the number of female responses to each male. We observed mating behavior with a blue filtered headlamp and recorded the times of initial male contact, and initiation of stages I and II of copulation. At this point, we collected focal females, males that mated successfully and unsuccessful dialoging males within the female dialog arena. When two or more males were observed simultaneously dialoging with a single female, these were termed competitive courtships and female responsiveness to each male could be determined as female response delay is consistent at a given temperature and competing male flashes did not overlap in time.

Each female's operational sex ratio was calculated as the maximum number of males observed dialoging within her dialog arena during the 5-min observation periods (Lewis & Wang 1991). In addition, each female's responsiveness was calculated as the proportion of all flashes within her dialog arena to which she responded. For cases in which the courtship dialog resulted in mating, we calculated female responsiveness to the mating male as well as to any other dialoging males. We conducted a paired t-test to explore differences in female responsiveness to the male with which it ultimately mated and the single most actively dialoging unsuccessful male. We used a stepwise multiple regression to examine the effects of day of season and local operational sex ratio on female responsiveness, and we conducted separate regressions to determine the effect of season on local operational sex ratio and duration of stage I because these data sets included females for which we had no responsiveness data. Female responsiveness was arcsine transformed for parametric analysis.

### Mating Success and Morphology

Field-collected *P. ignitus* were video-imaged and male and female elytra length, elytra width, pronotum width, eye span (distance across both eyes and intervening space), and lantern width and lantern area (maximum distance across lantern) were measured using NIH (National Institutes of Health) image. The male bioluminescent lantern occupies both the sixth and seventh abdominal sternites. As the sternites can overlap to a greater or lesser extent with the position

of the male's abdomen, lantern width was used to estimate male lantern size. Fireflies were weighed on a Mettler AT261 balance (Mettler-Toledo Columbus, OH, USA) to the nearest 0.1 mg. We reduced the number of body size measures using principal components analysis (PCA).

We categorized males and females according to mating outcomes in the field. Successful females were defined as females who attracted a male to initiate a stage I copulation that lasted for  $> 5$  min even if the copulation was disturbed later. Unsuccessful courting females were defined as females responding to artificial flashes that remained unmated by the end of the male flight period. Successful males included only those males that achieved stage II of copulation. Unsuccessful dialoging males were defined as males that dialoged with a female that eventually mated with another male. Unsuccessful courting males included these males as well as males collected at the end of the male flight period actively flashing as successful matings involve mate-guarding throughout the night. The size of successfully mated vs. unsuccessful courting males and females were compared using day of season as a covariate in a general linear model (GLM). We compared lantern widths of unsuccessful dialoging males with successfully mating males for males involved in competitive courtships using a t-test.

In addition many instances were observed in which a male contacted a female but did not mate. During 1995 and 1999, we distinguished three types of mating failures defined by female behavior and the initiation and length of stage I copulation: (1) In female-terminated matings, females walked away from the male immediately after contact; (2) in male-terminated matings, the pair made contact, but the male either did not initiate or terminated dorsal mounting (stage I of copulation) and broke contact within 5 min. In many cases, the male flew away and the same female failed to mate even when given the opportunity to mate with another male, (3) in mating failures, the male and female engaged in lengthy stage I copulation ( $\geq 1$  h) that never progressed to stage II (spermatophore transfer). Females involved in male-terminated matings ( $n = 9$ ) were frozen and dissected to count mature eggs ( $\geq 600$   $\mu\text{m}$  diameter) in the reproductive tract (ovaries and oviducts). During the same part of the season, successfully mating females ( $n = 14$ ) were collected and mature eggs counted. We compared the number of mature eggs in mated females and females involved in male-terminated matings using a Mann–Whitney U-test, because egg count data were not normally distributed. We also compared female elytron lengths between groups using a t-test.

### Male and Female Reproductive Investment

We assessed seasonal variation in male spermatophore mass which is correlated with protein content (Cratsley et al. 2003). We collected and weighed males and females over the entire mating season and placed pairs together in containers ( $n = 34$  1997 and 1998 combined). Pairs were separated 45 min after the beginning of stage II, the time required to complete spermatophore transfer. Females were immediately frozen to prevent degradation of the male spermatophore inside the female's reproductive tract. Intact spermatophores were dissected

from the female reproductive tract, rinsed briefly in distilled water, dried in a desiccation chamber and weighed on a Mettler M5 microbalance to the nearest 1  $\mu\text{g}$ . Mature eggs were also counted in the female reproductive tract to examine female reproductive investment. We used GLM to examine the effects of season and male body mass on spermatophore mass as well as on female body mass and egg count. To limit variation caused by seasonal differences when pooling our 1995–99 data, we defined early-season fireflies as any collected by day 15, and late-season fireflies as any collected beginning day 21 based on observations that sex ratio became increasingly female-biased by this time.

## Results

### Seasonal Changes in Courtship and Mating Behavior

Female flash responsiveness varied widely during the mating season, as well as among individual females on the same night. Female responsiveness to all male flashes ranged from 0 to 100% and increased significantly as local operational sex ratio (maximum number of males courting a female during 5-min observation periods) decreased (Fig. 1), but showed no clear pattern of change over the course of the season (Fig. 2) (stepwise multiple regression  $r^2 = 0.10$ , number of males:  $F = 5.52$ ,  $n = 39$ ,  $p = 0.024$ ; day of season: excluded, partial  $r = -0.253$ ,  $p = 0.12$ ). The local operational sex ratio decreased significantly over the mating season (linear regression,  $F = 20.18$ ,  $n = 75$ ,  $p < 0.001$ ; Fig. 3) indicating that fewer males were competing for access to females as the season progressed.

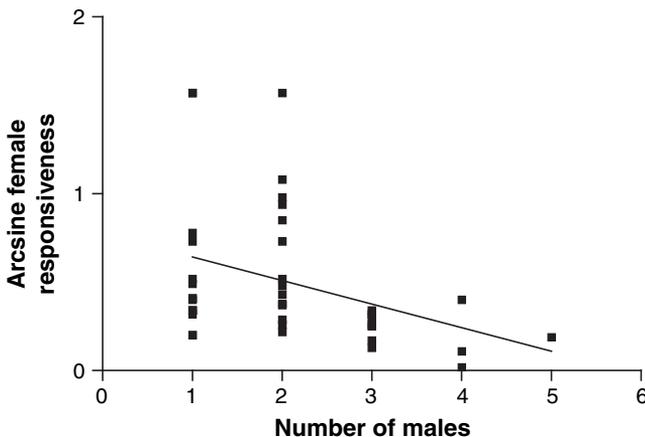


Fig. 1: Arcsine transformed proportion of *P. ignitus* male flashes to which females ( $n = 40$ ) responded as a function of maximum number of males flashing within 1 m of each female. Linear regression equation:  $y = -0.25x + 0.51$ ,  $r^2 = 0.13$

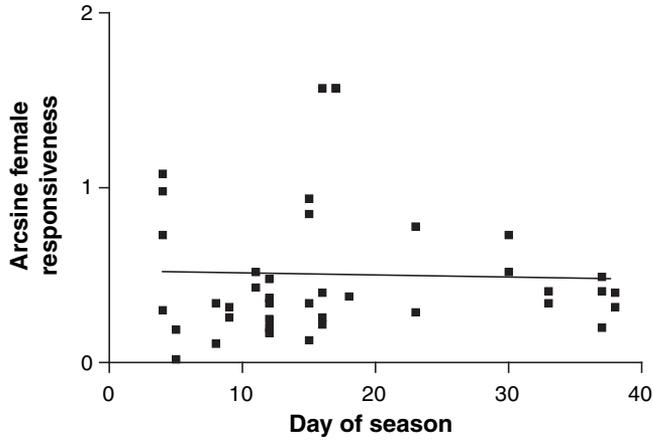


Fig. 2: Seasonal variation in arcsine-transformed proportion of *P. ignitus* male flashes to which females ( $n = 40$ ) responded. Linear regression equation:  $y = -0.01x + 0.28$ ,  $r^2 = 0.001$

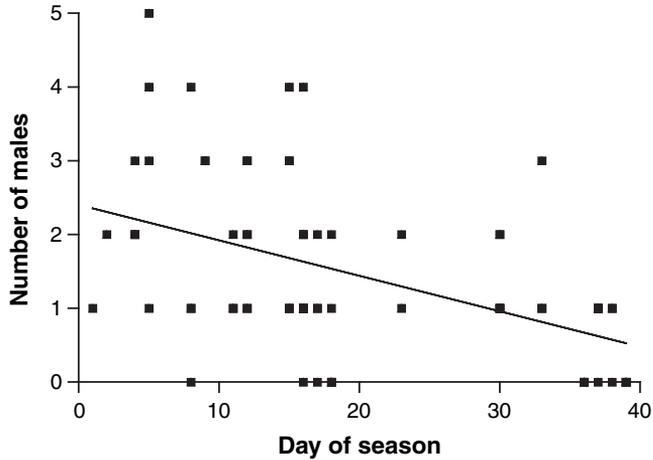


Fig. 3: Seasonal variation in local operational sex ratio for *P. ignitus* males dialoging within 1 m of each female ( $n = 76$ ). Linear regression equation:  $y = -0.05x + 2.4$ ,  $r^2 = 0.23$

### Female Flash Responsiveness

When two or more males courted a single female, females showed significantly higher responsiveness to the males with whom she eventually mated (female responsiveness to successful males  $\bar{x} \pm \text{SE} = 65.3 \pm 12.6\%$ , female response to unsuccessful males  $\bar{x} \pm \text{SE} = 33.3 \pm 13.9\%$ , paired t-test,  $t = 2.9$ ,  $df = 6$ ,  $p = 0.027$ ).

In successful matings, the duration of stage I varied from 30 s to 43 min, with no clear seasonal pattern (linear regression,  $r^2 = 0.02$ ,  $n = 22$ ,  $p = 0.42$ ).

Male–female contact led to successful stage II copulation in 70% of courtship interactions observed ( $n = 47$ ). In those courtships that did not lead to stage II of copulation, we observed two cases of female-terminated matings, eight male-terminated matings and two other mating failures. Male-terminated matings occurred during the latter half of the early season through late season.

### Mating Success and Morphology

*Photinus ignitus* morphological characteristics in both males and females were reduced to a single principal component of ‘size’ that accounted for over 70% of the variance (Table 1). Male body size did not differ between successfully mated and unsuccessful courting males, but there was a significant effect of day of season on male body size as body size decreased over the course of the season (GLM: mating success,  $F = 0.062$ ,  $p = 0.8$ ; day of season,  $F = 4.82$ ,  $p = 0.03$ ; Fig. 4a). However, males that successfully mated in competitive courtships (two or more dialoging males) had significantly wider lanterns ( $\bar{x} \pm SE = 2.37 + 0.06$  mm) than unsuccessful dialoging males ( $\bar{x} \pm SE = 2.14 + 0.07$  mm, t-test,  $t = -2.6$ ,  $df = 10$ ,  $p = 0.03$ ).

Successfully mating *P. ignitus* females had significantly larger body sizes than unsuccessful females and there was a significant effect of day of season on female body size (GLM: mating success,  $F = 5.47$ ,  $p = 0.02$ ; day of season,  $F = 7.30$ ,  $p = 0.01$ ; Fig. 4b). Females involved in male-terminated matings had significantly fewer eggs (median 3, range 1–33,  $n = 9$ ) than successfully mating females (median 17.5, range 7–60,  $n = 14$ ) (Mann–Whitney  $U = 108.5$ ,  $p = 0.004$ ). This was not because of body-size differences, as elytra length did not differ between the two groups of females (t-test,  $t = -0.394$ ,  $n = 9$  and 14,  $p = 0.177$ ).

### Seasonal Change in Male and Female Reproductive Investment

The relationship between male body mass and spermatophore mass changed between early vs. late season (GLM:  $n = 34$ , season \* body mass:  $F = 8.1$ ,

Table 1: Factor loadings for the first component of a principal components analysis of six size traits in males and females

	Male component 1 ‘size’	Female component 1 ‘size’
Eigenvalue	4.94	4.19
Proportion of variance	0.71	0.70
Variable		
Mass	0.664	0.553
Elytron length	0.773	0.891
Elytron width	0.499	0.608
Pronotum width	0.790	0.784
Eye span	0.844	0.787
Lantern width/area (male/female)	0.647	0.571

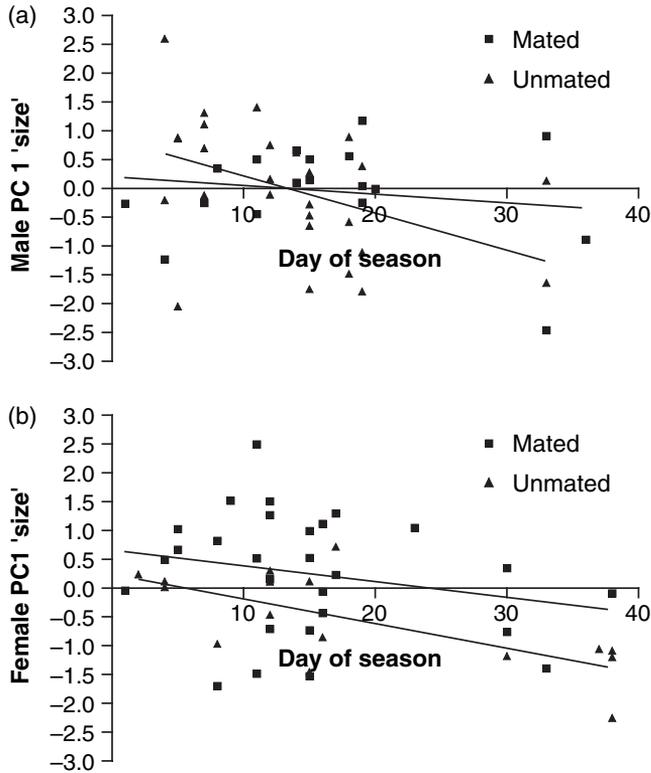


Fig. 4: Body size (PC1) of successfully mating and unsuccessful courting *P. ignitus* over the course of the season; (a) males (n = 45); (b) females (n = 44)

$p = 0.008$ ; Fig. 5a). Body mass predicted a significant proportion of the variation in spermatophore mass (GLM,  $n = 34$ , body mass:  $F = 31.5$ ,  $p < 0.001$ ), but this relationship was stronger for early-season males ( $r^2 = 0.69$ ,  $n = 14$ ) than for late-season males ( $r^2 = 0.23$ ,  $n = 20$ ). Males collected during late season produced significantly smaller spermatophores ( $\bar{x} \pm SE = 58.2 + 5.7 \mu\text{g}$ ) than males collected during early season ( $\bar{x} \pm SE = 103.0 + 16.7 \mu\text{g}$ ) (GLM:  $n = 34$ , season:  $F = 7.8$ ,  $p = 0.009$ ).

Female egg number increased with increasing female body mass during both early and late seasons (GLM:  $n = 56$ , body mass:  $F = 65.6$ ,  $p < 0.001$ ; Fig. 5b). There was no significant difference in egg numbers across seasons and no effect of season on the relationship between body mass and number of eggs (GLM:  $n = 56$ , season:  $F = 0.6$ ,  $p = 0.428$ ; season \* body mass:  $F = 1.0$ ,  $p = 0.326$ ).

## Discussion

Our results suggest major behavioral shifts in *P. ignitus* mating behavior that correspond with seasonal changes in both operational sex ratio and reproductive

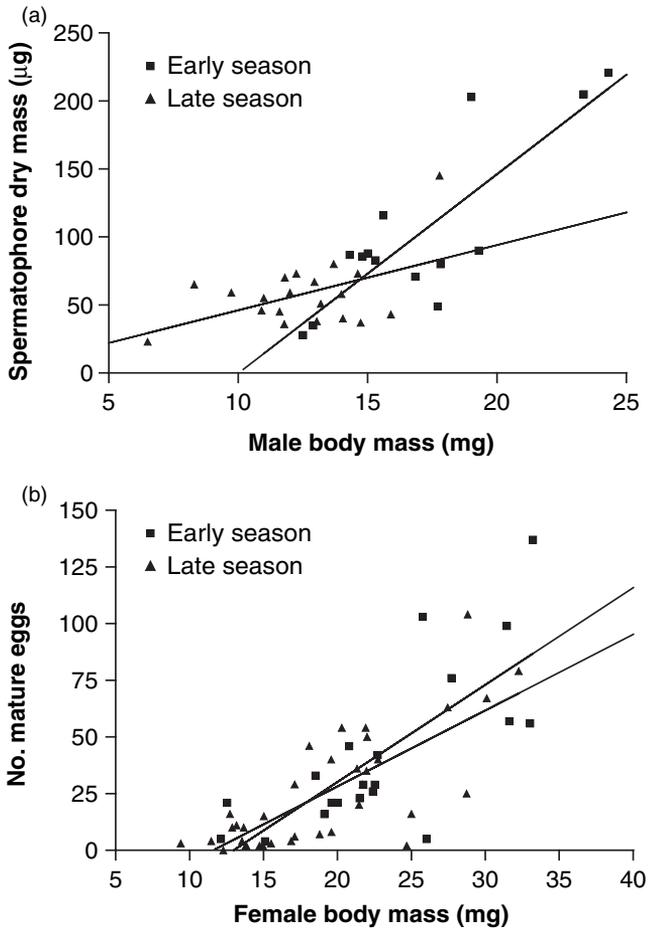


Fig. 5: Seasonal changes in male and female reproductive investment. (a) Male *P. ignitus* spermaphore dry mass as a function of wet body mass for early season (Jun 22 to Jul 6;  $n = 14$ ) and late season (Jul 12 to Aug 5;  $n = 20$ ) males. (b) Number of mature eggs in *P. ignitus* female reproductive tracts as a function of body mass for early season (Jun 22 to Jul 6;  $n = 20$ ) and late season (Jul 12 to Aug 5;  $n = 34$ ) females

investment. *P. ignitus* sex ratio becomes less and less male biased as the season progresses. When females engaged in courtship dialogs with multiple males, female responsiveness to male flashes was low. This suggests that females become more selective when male availability is high and the probability of a lost mating opportunity is low. During competitive courtships (two or more males), *P. ignitus* females showed higher responsiveness to flashes from particular males, and these were the males that subsequently went on to successfully mate with the female. Preferential female responsiveness directed toward the male with which the female eventually mates, as well as changes in female responsiveness over the course of

the season have also been shown for *P. aquilonius* and *P. marginellus* fireflies (Lewis & Wang 1991).

Preferential female response may reflect intrinsic differences among courting males. Female responsiveness has previously been shown to depend on male flash behavior, specifically male flash duration in *P. ignitus* (Cratsley & Lewis 2003), and male pulse rate in *P. consimilis* (Branham & Greenfield 1996). Although male flash traits were not measured in the present study, males that were successful in competitive courtships had greater lantern widths than their unsuccessful counterparts. This is consistent with results from previous work, which found that *P. ignitus* females show higher responsiveness to larger artificial lanterns (Cratsley & Lewis 2003). However, our results differ from those of VencI & Carlson (1998), who found *P. pyralis* males that successfully mated in the presence of three or more competitors had smaller lanterns and body sizes; only in the absence of competitors did successful *P. pyralis* males have larger lanterns and body sizes compared with the population mean. Male-male interference competition may be more intense in *P. pyralis*, where males form 'love knots' consisting of many males surrounding a single female (Mauer 1968), and this may explain the different effects of lantern size between these two species.

Firefly courtship may also involve female mate competition and male mate choice. *P. ignitus* females that successfully mated had larger body size compared with unsuccessful females. Larger size-related traits such as eyespan and lantern area may enhance females' ability to detect male flashes and produce attractive response flashes. These traits along with increased responsiveness may help females compete in attracting potential mates. In addition, the occurrence of male-terminated matings during the latter part of the early season and through the late season suggests the possibility of male choice. During these aborted matings, males contacted females but then terminated mating before or during the dorsal mounting stage of copulation (stage I), prior to spermatophore transfer. Females involved in male-terminated matings had significantly fewer mature eggs in their reproductive tracts than successfully mating females. These results suggest that males can assess female reproductive potential, perhaps during dorsal mounting (stage I), and choose to mate with the most fecund females. Our finding that successfully mated females had larger body masses (indicating more eggs) than unsuccessful females is also consistent with male mate choice of females with higher reproductive potential. This sort of male choice as a function of female fecundity occurs in many insects mating systems where females receive cumulative benefits from costly male investments at mating (Bonduriansky 2001).

This research also suggests that seasonal changes in male spermatophore quality may influence *P. ignitus* courtship and mating behavior. In this study, males collected during late season produced significantly smaller spermatophores than early season males. Our previous work has shown that in *P. ignitus* male spermatophore mass declines across successive matings, and that the cost of spermatophore production can limit male mating opportunities (Cratsley et al. 2003). In *Kawanaphila nartee* katydids a shift in operational sex ratio has been

attributed to changes in food plant availability to males for spermatophore production (Gwynne & Simmons 1990; Simmons & Bailey 1990). Because *Photinus* fireflies do not feed as adults, declining spermatophore size likely reflects diminishing nutritional reserves available for spermatophore production. Therefore, while early in the season males may benefit by mating as frequently as possible, limits on spermatophore production may cause males to become increasingly selective about their mates later in the season.

Our results support the potential for variation in both the costs and benefits of mate choice to maintain behavioral plasticity within a species. Variation in mating behavior may occur in many other species in which males make substantial nutrient contributions at mating. Future studies in other species should explore how nuptial gifts influence the costs and benefits of mate choice, as well as how variation in these costs and benefits affect courtship behavior in the field.

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