

# Mate recognition and choice in *Photinus* fireflies

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This paper offers a view of firefly mate recognition and choice seen through the lens of recognition system theory. We review the expression and perception of firefly bioluminescent signals, and describe the photic cues used by *Photinus* fireflies (Coleoptera: Lampyridae) in the processes of species recognition (identifying conspecifics) and mate-quality recognition (discriminating among potential conspecific mates). The signal characters used by *Photinus* females to discriminate among potential mates include flash pulse rate and pulse duration, similar temporal characters to those assessed by females in acoustically signaling insects. We also review male nuptial gift production and transfer, and describe the relationship found between male flash signals and nuptial gift size for *Photinus ignitus*. We present evidence of mate choice by *Photinus* males, which appear to allocate limited resources by rejecting low fecundity females. We assess the potential for postcopulatory female choice to mediate mate acceptance errors by increasing paternity success of higher quality mates, or blocking fertilizations by low quality mates. Finally, we integrate recognition system and mate choice theoretical approaches to develop predictions concerning how various factors will alter both male and female mate acceptance thresholds for *Photinus* fireflies.

## Introduction

The courtship signals and responses used to recognize and choose among potential mates can be viewed within the framework of recognition systems as encompassing three components (Reeve 1989, Sherman *et al.* 1997, Starks 2004): expression, perception, and action. To comprehend the expression component, we need to identify which signals are used in species and mate-quality recognition, and to understand how these signals are generated (*see* Tsutsui 2004). The perception component involves the evaluator's peripheral and central signal processing, including matching incoming signals with

the evaluator's internal recognition templates (*see* Mateo 2004). Lastly, the action component describes how the evaluator responds to template matching, for example females' emitting their own response signal or moving toward a potential mate (*see* Liebert & Starks 2004). Because nocturnal firefly courtship is generally based on highly visible bioluminescent signals, these insects should be particularly amenable to studies of mate recognition and choice.

In many firefly species and other taxa where females mate with multiple males, sexual selection continues during and after copulation. Females may influence which of several mating males will sire their offspring (Eberhard 1996),

and males may strategically allocate limited resources among females (Simmons 2001). Such peri- and post-copulatory choice is likely to rely on signals in entirely different sensory channels than pre-copulatory choice, and such multi-modal information has the potential to provide more reliable assessments of mate quality.

Reeve's (1989) optimal acceptance threshold model provides a useful framework for studying plasticity of pre-mating choice, and could be extended to include post-mating choice. The central problem for mate recognition is to identify an acceptance threshold that optimally balances two types of discrimination errors: rejection error (in this context, rejecting a suitable mate) and acceptance error (accepting an unsuitable mate). These reciprocally-related discrimination errors are analogous to type I and type II errors in statistical hypothesis-testing, and likewise the optimal balance will depend on the consequences (costs) of making such errors. Major factors likely to influence the consequences of mate discrimination errors include ecological factors impacting mate search costs, such as operational sex ratios and predation intensity, as well as various factors that alter fitness gains, such as mate quality distributions and evaluator condition. Peri- and post-copulatory female choices have the potential to be critical steps in mate quality assessment, because these processes may allow females to rectify previous mate choice acceptance errors.

In this paper, we briefly review the expression and perception components of firefly flash signals; the physiological basis of flash production and sensory perception have been comprehensively reviewed elsewhere (Case 1984, Carlson & Copeland 1985). We then discuss the photic signaling system used in species recognition and mate-quality recognition in North American *Photinus* fireflies (Coleoptera: Lampyridae), a group that has been particularly well-studied. Although similar bioluminescent signals are used for sexual advertisement and courtship in other lampyrids, many variants of photic and pheromonal communication systems exist in this family (Lloyd 1997, Branham & Wenzel 2003, Ohba 2004). We next review what is currently known about pre-mating choice in *Photinus* fireflies, and discuss the potential for post-copula-

tory choice. Finally, we present an integrated conceptual framework that incorporates both pre-copulatory and post-copulatory choices, and offer some predictions about factors likely to influence mate quality acceptance thresholds in both sexes.

## Expression and perception of bioluminescent signals

A comprehensive cladistic analysis of the beetle family Lampyridae indicates that nocturnal activity and bioluminescent sexual signals are derived traits, as basal taxa are diurnal and mainly rely on pheromones for sexual communication (Branham & Wenzel 2003). However, many extant species consist of flashing fireflies that use discrete bioluminescent flashes during sexual advertisement and courtship to convey information concerning species identity, sex, and mate quality. These precisely timed flashes are produced within an abdominal lantern by chemiluminescent reactions that are fueled by oxygen and ATP (reviewed by Wilson & Hastings 1998). Only adult fireflies are capable of such precise on-off flash control, and adult lanterns show several anatomical features absent from larval lanterns (Ghiradella 1998). Bioluminescent sexual signaling in the Lampyridae appears to be an exaptation originating from the glows produced by larval lanterns, which continue to function as an aposematic warning display for unpalatable larvae (Branham & Wenzel 2003, De Cock & Matthyson 2003). In adult fireflies, a flash is triggered by neural impulses that stimulate synaptic release of the neurotransmitter octopamine in the firefly lantern. Recent work suggests that octopamine release causes a transient increase in production of nitric oxide, a rapidly diffusing gas that may switch on the flash by allowing oxygen to reach the luciferin-luciferase reactants housed within the lantern photocytes (Trimmer *et al.* 2001, Aprille *et al.* 2004). Thus, adult firefly lanterns are both anatomically and physiologically specialized to produce the precisely timed photic signals used in sexual communication.

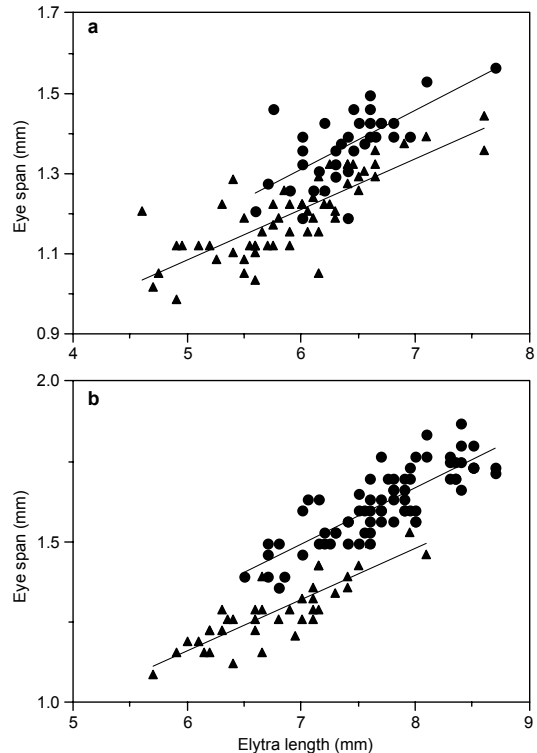
Signal detection ability is enhanced by several anatomical features of firefly eyes (reviewed by Case 1984). Like most night-active insects,

fireflies have superposition eyes, in which a clear zone between the corneal lens and the sensory components increases light-gathering potential. Furthermore, eye size is sexually dimorphic in many fireflies, with males having considerably larger eyes than females of the same species (Case 1984; Fig. 1). Since larger eyes are correlated with smaller interommatidial angles, this suggests that males are subject to stronger selection than females for visual resolution and/or accurate distance perception.

Signal-to-noise ratios are maximized for detection of conspecific flashes by close spectral tuning between each species' visual sensitivity peak and its bioluminescence emission (Lall *et al.* 1980a, Case 1984). Noise is also minimized by a spectral shift toward yellow flashes among crepuscular species, in contrast to the green flashes produced by fully nocturnal species. This pattern suggests selection for increased signal detection at dusk against an ambient background that includes green foliage (Lall *et al.* 1980b). In *P. pyralis*, females appear to use a single chromatic receptor to detect conspecific males, indicating that flash color is unlikely to be an important parameter in *Photinus* signaling systems (Lall & Worthy 2000). A close correspondence between the compound eye's electroretinographic spectral sensitivity and the action spectrum of *Photinus* females' behavioral flash response (Case 1984, Lall & Worthy 2000) indicates a tight linkage between female flash perception and female action components.

### ***Photinus* flash signaling and species recognition**

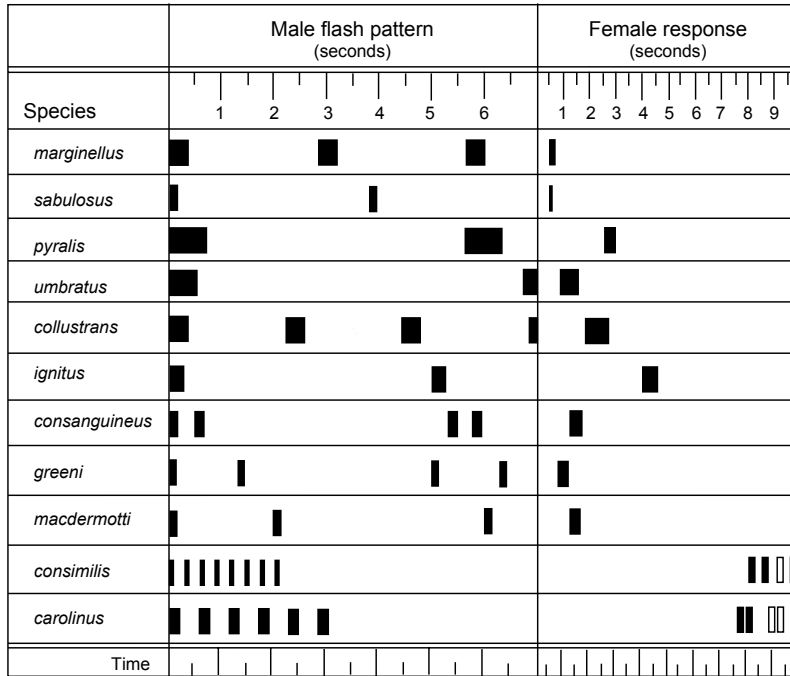
The spectacular bioluminescent displays of *Photinus* fireflies consist of sexual advertisement flashes produced by roving males to locate sedentary females (Lloyd 1966; Fig. 2). Thus, *Photinus* males act both as primary signalers and as searchers. These species-specific, temperature-dependent male flash signals are temporally coded, a feature shared with the acoustic and vibratory signals used in courtship by many insects (Greenfield 2002). Male signals in most North American *Photinus* species consist of a single pulse ranging from 100 to 750 msec dura-



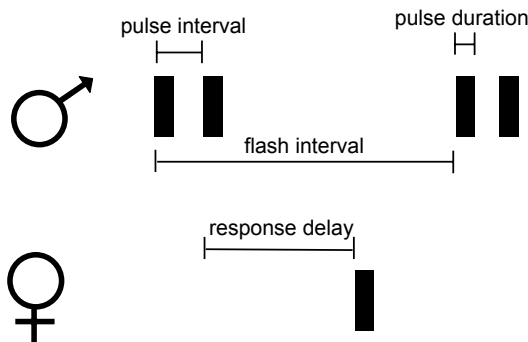
**Fig. 1.** Sexual dimorphism in eye size for (a) *Photinus marginellus* and (b) *Photinus aquilonius*. For both species, eye span (measured as distance between outer margins of left and right eyes) is shown relative to elytra length for males (circles) and females (triangles).

tion that is repeated at fixed intervals. In other species, males emit multiple-pulsed flash patterns consisting of two to several short pulses delivered at various rates, with flash patterns again repeated at fixed intervals (*see* Fig. 3 for terminology). The action component of the female response to an appropriate male signal consists of a single response flash given at a species-specific time delay; in a few *Photinus* species, this female response contains multiple pulses (Fig. 2).

Sympatric *Photinus* species often differ in their breeding habitats, mating seasons, or time window occupied by their nightly flight periods (Lloyd 1966). In addition to these spatial and temporal isolating mechanisms, flash pattern specificity among co-occurring species suggests that there has been reproductive character displacement on the expression component of firefly flash signals to reduce interspecific dis-



**Fig. 2.** Species differences in *Photinus* male flash signals (left) and female response flashes (right; note different time scales). Female flash responses are timed from initiation of the last pulse in the male flash pattern (open symbols indicate optional responses). Signal timing is temperature-dependent, so timing shown is approximate (temperatures ranging from 19–24 °C). Modified from Lloyd 1966, with additional data from Lloyd 1969, Branham & Greenfield 1996, Copeland & Moseiff 1995.



**Fig. 3.** Terminology used to describe *Photinus* flash signals (based on Lloyd 1966).

crimination errors (Lloyd 1966, 1997). *Photinus* fireflies recognize conspecific signals based primarily on temporal characteristics of the male flash pattern, rather than other signal attributes such as flash color, flash kinetics, or spatial gesture (Buck 1937, Lloyd 1966). *Photinus* females have been shown to identify males of their own species based on pulse duration, pulse rate, and pulse number, while males identify conspecific females on the basis of female response delay (Buck 1937, Lloyd 1966, Case 1984, Carlson & Copeland 1985).

Although most *Photinus* females are capable of flight, during courtship they respond to male signals from perches in vegetation; a few species have brachypterous females that cannot fly. When a male detects a female reply, he moves toward her and signals again. The male generally lands after a few flash exchanges, and the flash dialog continues as he approaches the female on foot. Courtship dialogs appear to involve only visual cues, as females in airtight containers as well as males lacking antennae engage in normal dialogs (Lloyd 1966, Carlson & Copeland 1978). However, there is anecdotal evidence that once males contact a female, chemical or tactile signals may be used for short-range species discrimination (Lloyd 1966).

Some intriguing departures from the flash signaling system described above occur in certain *Photinus* species. In *P. macdermotti*, males emit one flash pattern during patrolling flight and switch to a different flash pattern during courtship (Lloyd 1969, Carlson *et al.* 1976). In *P. carolinus* and *P. knulli*, males within a population temporarily synchronize their flash signals while searching for females (Cicero 1983, Copeland & Moseiff 1995). As in the case of mass synchrony by sedentary males in southeast Asian *Pteroptyx fireflies*

(Buck 1938, 1988), the role of such synchrony in species recognition, mate competition, and mate choice remains a fascinating area of study.

## Intraspecific signal variation and female mate choice

As discussed above, *Photinus* females use male flash advertisements to identify conspecific males. Females also discriminate among males of their own species, and such discrimination appears to be based on some of the same flash signal characters shown to be important in species recognition. Thus, species recognition and mate-quality recognition may not represent distinct processes in fireflies, but rather a continuum (Ryan & Rand 1993).

Prior to mating, *Photinus* females have multiple opportunities to assess male flash signals. Male flight periods in most species last ~1 h, and male–female courtship dialogs after males have landed often continue for more than an hour (Carlson *et al.* 1976, Lloyd 1979). These ongoing dialogs attract additional males, and under the male-biased sex ratios typical of early mating season, females may attract a small coterie of suitors (Vencl & Carlson 1998). During courtships involving several males, females show preferential response to particular conspecific flashes, and signaling females often aim their

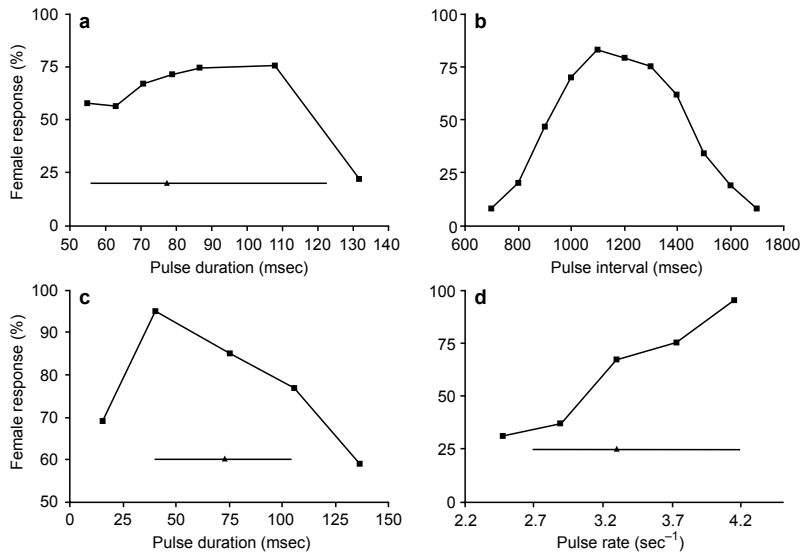
abdominal lantern toward a specific male (Lloyd 1966, Buck & Buck 1972, Vencl & Carlson 1998). Studies have shown that in these competitive courtships, males that end up mating are the ones that elicit more female flash responses (Lewis & Wang 1991, Vencl & Carlson 1998, Cratsley & Lewis 2004). Flash dialogs continue until the male and female make physical contact, after which mounting usually takes place immediately; under some circumstances males may reject females (*see below*), but only rarely do females reject males after contact. Since copulations last beyond the male flight period, both sexes are limited to a single mating each night. Thus, female mate choice involves perception and assessment of male flash signals, with preferential response based on signal characters.

Although relatively few species have been studied in detail (Table 1), considerable intraspecific variation in male signal characters has been found to underlie the species-specificity of *Photinus* flash codes (Carlson & Copeland 1985, Cratsley 2004). Pulse duration varies among males in the single-pulse flash patterns of *P. pyralis* and *P. ignitus* (Cratsley 2000, Cratsley & Lewis 2003), as well as in *P. consimilis*, a species in which males produce multiple-pulse flash patterns (Branham & Greenfield 1996). In *P. greeni* and *P. macdermotti*, male signals consist of paired pulses (Fig. 2), and males exhibit different interpulse intervals (Buck & Buck 1972, Carlson

**Table 1.** Summary of evidence from different *Photinus* fireflies concerning whether particular male bioluminescent flash characters demonstrate intraspecific variation, female discrimination among signals within their species range, and correlation with male nuptial gift size.

	Male flash characters	
	Pulse duration	Pulse rate
<b>Evidence for:</b>		
<b>Intraspecific variation</b>	<i>P. consimilis</i> <sup>1</sup> <i>P. ignitus</i> <sup>2</sup>	<i>P. consimilis</i> <sup>1</sup> <i>P. greeni</i> <sup>4</sup> <i>P. macdermotti</i> <sup>5</sup>
<b>Female preference</b>	<b>For longer duration:</b> <i>P. ignitus</i> <sup>2</sup> <i>P. pyralis</i> <sup>3</sup>	<b>For faster pulse rate:</b> <i>P. consimilis</i> <sup>1</sup> <b>For intermediate pulse rate:</b> <i>P. greeni</i> <sup>4</sup> <i>P. macdermotti</i> <sup>5</sup>
<b>Correlation with nuptial gift</b>	<i>P. ignitus</i> <sup>2</sup>	no data

<sup>1</sup>Branham & Greenfield 1996, <sup>2</sup>Cratsley & Lewis 2003, <sup>3</sup>Cratsley 2000, <sup>4</sup>Buck & Buck 1972, Buck & Case 1986, <sup>5</sup>Carlson *et al.* 1976.



**Fig. 4.** Female preference (measured as % response) for flash characters tested with artificial photic stimuli: — **a:** *Photinus ignitus* pulse duration; — **b:** *P. greeni* interpulse interval; — **c:** *P. consimilis* pulse duration; — **d:** *P. consimilis* pulse rate. Horizontal lines and triangle indicate population range and mean for male flash characters (modified from Buck & Case 1986, Branham & Greenfield 1996, Cratsley & Lewis 2003).

et al. 1976). *P. consimilis* males also differ in their pulse rates (Branham & Greenfield 1996). There may be also be intraspecific variation in other flash characters, such as spatial gesture and flash kinetics (rate of intensity rise and decay), but these attributes have not yet been examined.

The signal characters used by females to discriminate among potential mates have been isolated using photic playback experiments in several *Photinus* species (Fig. 4). In two species with single-pulse male signals, *P. ignitus* and *P. pyralis*, females respond preferentially to flashes with longer pulse durations (Cratsley 2000, Cratsley & Lewis 2003), although female response rates decline for signal durations that lie outside the conspecific range (Fig. 4a). In those *Photinus* species with multiple-pulse male signals, females appear to discriminate on the basis of pulse rate, rather than pulse duration. In *P. consimilis*, females show higher response rates to signals with faster pulse rates (Fig. 4d), and their response flashes contain more pulses (Branham & Greenfield 1996, Greenfield 2002). *P. consimilis* females appear less sensitive to differences in pulse duration (Fig. 4c). Females also respond differentially to signals with varying interpulse intervals in *P. macdermotti* (Carlson et al. 1976) and *P. greeni* (Buck & Buck 1972, Buck & Case 1986); in these species, signals with intermediate interpulse intervals appear to be preferred (Fig. 4b). In testing situations, *Photinus* females have

also been shown to respond preferentially to higher intensity flash signals (Vencl & Carlson 1998, Cratsley 2000, Cratsley & Lewis 2003). However, because perceived intensity varies with male distance, females could only use flash intensity to assess male quality when they also have reliable distance information; while fully nocturnal species would lack such distance cues, they might be present in crepuscular species. *P. pyralis* females also respond preferentially to the leading signal when simulated male flashes are presented out of synchrony (Vencl & Carlson 1998), but additional work is needed to see whether males vary consistently in their tendency to produce either a leading or lagging signal.

Species recognition and mate-quality recognition operate simultaneously as agents of selection on male signaling traits, and the shape of female preference functions may provide some insight into the relative importance of these processes (Ryan & Rand 1993). In the context of species recognition, female preference functions are expected to be unimodal, favoring male signals closer to the population mean as females are selected to minimize acceptance errors. However, in mate quality contexts, females often choose male signals above the population mean (Andersson 1994, Sherman et al. 1997). Female preferences for longer male pulse durations (*P. ignitus*, *P. pyralis*) and faster pulse rates (*P. consimilis*) above their respective population

means are consistent with this pattern. In these instances, female mate choice produces directional selection on male flash characters, which may be balanced at the upper end by selection for species recognition. Based on female preference functions, female discrimination of interpulse intervals in *P. greeni* and *P. macdermotti* may serve mainly for species recognition, although further work is needed to determine the range of natural intraspecific variation in this species complex. In general, the degree of spatial and temporal overlap between firefly species should determine the relative importance of species *vs.* mate recognition errors in flash signaling systems. Additional studies of female preference functions (e.g. Branham & Greenfield 1996, Cratsley & Lewis 2003) should provide further insight into these processes.

In summary, *Photinus* fireflies appear to rely on the photic equivalents of many of the same temporal signal characters that are involved in mate choice of acoustically signaling insects. In many insects, females prefer longer signals and higher signal rates, perhaps revealing a general preference for high energy male signals (Greenfield 2002). Assuming that high energy signals are costly (e.g. require greater metabolic expenditure or incur greater predation risk), such male signals may act as honest indicators of male genetic quality and/or phenotypic condition.

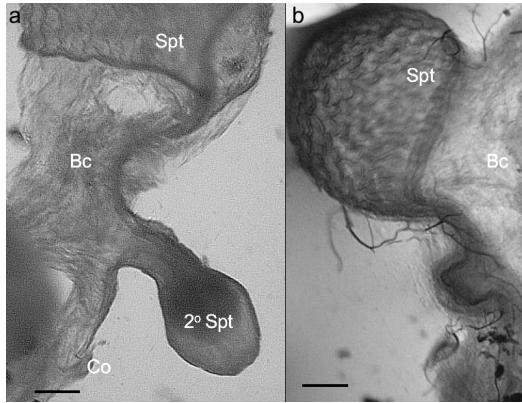
### Male nuptial gifts and female assessment of mate quality

In the context of mate choice, male signal variation may be used to assess a male's quality on the basis of indirect benefits (genetic quality or compatibility) or direct benefits (resources). Direct benefits may be of particular economic importance in *Photinus* fireflies, because most species lack adult feeding (Lloyd 1997). Thus, all the energy required for reproduction needs to come from resources acquired as larvae. *Photinus* males provide a nuptial gift to females consisting of a protein-rich spermatophore that is transferred internally during copulation (van der Reijden *et al.* 1996, Lewis *et al.* 2004). In *P. ignitus*, females allocate the majority of spermatophore-derived protein to provision their developing oocytes

(Rooney & Lewis 1999), and this nutritional contribution results in increased fecundity for multiply-mated females (Rooney & Lewis 2002). Based on this direct fitness benefit, *Photinus* females are expected to continue foraging for matings even after they have acquired sufficient sperm to fertilize their eggs. Male spermatophore size is likely to be an important aspect of male quality. While females in many gift-giving insects can directly evaluate externally presented nuptial gifts (Andersson 1994), female fireflies appear to rely on male flash signals to predict nuptial gift size (Cratsley & Lewis 2003, Cratsley 2004). In *P. ignitus*, males producing courtship flashes with longer durations also deliver larger spermatophores, indicating that at least in this species, temporal flash characters can serve as an honest indicator of mate quality based on material resources. Of course, this material fitness gain does not preclude the possibility of genetic benefits from mate choice; for example, males producing larger spermatophores may also be genetically superior in terms of their larval resource acquisition ability.

### Female fecundity and male assessment of mate quality

When males face constraints on reproductive resources, selection is also expected to favor male mate choice (Bonduriansky 2001, Simmons 2001). *Photinus* males show a monotonic decline in spermatophore size across consecutive matings (Cratsley *et al.* 2003), indicating that older males have limited resources available for reproduction. Whereas early in the mating season *Photinus* males almost always proceed to copulate with any female they contact, later males can be seen to reject certain females after antennating and mounting them. These rejected females were found to have significantly fewer eggs in their ovaries as compared with the females accepted as mates (Cratsley & Lewis 2004). These observations suggest that older firefly males might assess several potential mates, and allocate their limited resources by rejecting any females with low fecundity. Male mate choice in other insects often relies on tactile or chemical cues (Bonduriansky 2001), and male fireflies may use abdominal curvature to assess female fecundity.



**Fig. 5.** Differences in female reproductive tract anatomy between (a) *P. greeni* and (b) *P. ignitus*. In both species, males deposit their spermatophore in the female's bursa copulatrix (Bc). Sperm is stored in the primary spermatheca (Spt). *P. greeni* females have evolved an additional structure for sperm storage, the secondary spermatheca (2° Spt), which is situated closer to the entrance of the common oviduct (Co) where fertilization occurs. Scale bars = 200  $\mu$ m.

## Potential for post-copulatory choice

In species where both sexes mate multiple times, several additional action components may take place during or after copulation. Cryptic female choice refers to females differentially accepting, storing, or using sperm from particular mates (Eberhard 1996, Simmons 2001). Unlike longer range advertisement and courtship signals, recognition cues produced and perceived during copulation (known as copulatory courtship) are likely to use short-range chemical, tactile, or vibratory channels (Eberhard 1991). These cues may provide additional information about mate quality, which females could use to increase the paternity success of higher quality mates, or to block fertilizations by lower quality mates. In several other insects, including *Dryomiza* flies (Otronen 1997), *Tribolium* flour beetles (Edvardsson & Arnqvist 2000), and *Diabrotica* cucumber beetles (Talamy 2003), male behaviors during copulation have been shown to be associated with increased male paternity success. Males may also alter their allocation of sperm or accessory gland products during copulation in response to differ-

ences in female reproductive status or fecundity (Bonduriansky 2001). This strategic allocation of male resources has been called cryptic male choice (Simmons 2001), and is likely to evolve in species with high male mating effort or parental investment. Thus, both sexes may use peri- or post-copulatory mate-quality recognition to fine-tune their previous mate choice decisions.

In most *Photinus* species studied to date, females mate with multiple males (the monandrous females of *P. collustrans* are an exception; Wing 1984), so the potential exists for post-copulatory female choice. In addition, the presence of male nuptial gifts is expected to select for females to mate multiply to gain material benefits, and subsequently exercise post-copulatory choice. *Photinus* females might assess the quality of a male, or his spermatophore, through tactile or chemical signals exchanged during prolonged copulations, which can last up to 8 hours (Wing 1985, Lewis & Wang 1991). Females' ability to determine fertilization outcomes will be influenced by their reproductive morphology. In other insects, females are able to differentially store sperm from several mates in multiple sperm storage organs within the reproductive tract (Hellriegel & Bernasconi 2000). Among *Photinus* species there are some striking differences in female reproductive morphology (Fig. 5). After mating, sperm are typically stored in a spherical storage organ, the spermatheca, which is located at the anterior end of the reproductive tract. In *P. greeni*, females have an additional site for sperm storage (the secondary spermatheca) located closer to the oviduct entrance, the presumed site of egg fertilization. If *Photinus* females can differentially store sperm in these compartments, this could bias paternity toward particular mates. Cryptic male choice might be accomplished by males adjusting the size of their spermatophore after assessing female condition; opportunity for such male adjustments exist as spermatophore components are assembled within the male reproductive tract and transferred during the first 30 min of copulation (van der Reijden et al. 1997). Studies are currently underway to determine the extent to which female post-copulatory choice and male cryptic choice occur, as well as what signals might be involved.



## Firefly mate choice and recognition systems

A central focus in recognition systems is locating an acceptance threshold that optimally balances acceptance and rejection errors in a dichotomous choice situation between suitable and unsuitable mates that have overlapping cue-dissimilarity distributions (Reeve 1989, Sherman *et al.* 1997). The optimal acceptance threshold model for 'search-and-settle' actors (evaluators) predicts that the optimal threshold for template-recognition cue dissimilarity will become less restrictive with either: (1) decreased fitness benefit from accepting a desirable recipient (cue-bearer), or (2) increased search cost.

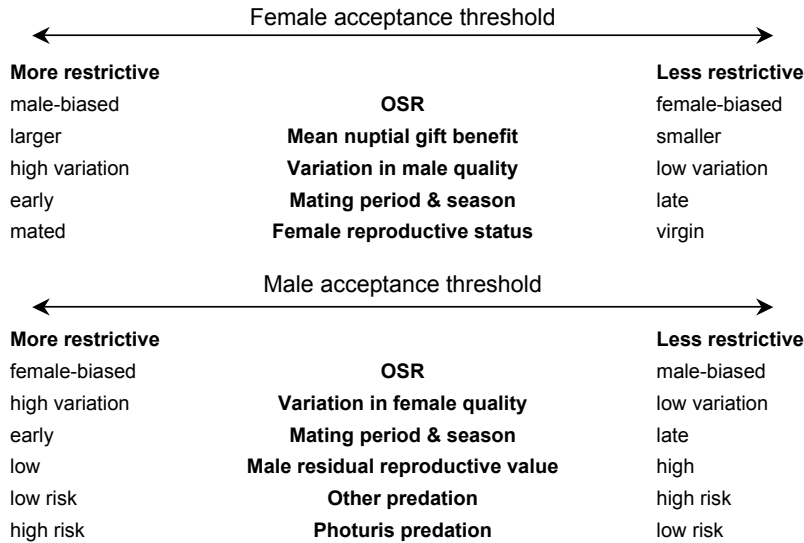
Mate choice theory offers a complementary perspective on factors influencing acceptance thresholds when such thresholds are situated along a continuous distribution of mate quality (Parker 1983, Real 1990, 1991, Gibson & Langen 1996, Jennions & Petrie 1997, Johnstone 1997). In both recognition system and mate choice theoretical frameworks, increased search costs are predicted to lead to lower mate selectivity (Parker 1983, Reeve 1989, Real 1990). Search costs can either be direct (search time, energy expenditure, and predation risk) or opportunity costs, such as lost mating opportunities (Real 1990). Mate choice theory also considers several relevant parameters likely to affect fitness gains from choice. One such parameter is variance in mate quality distributions, with increased variance predicted to increase acceptance thresholds (Parker 1983, Real 1990). In models of sequential mate search with time constraints, the mate-quality threshold is predicted to decline as the mating period or mating season progresses (Real 1990, Johnstone 1997). Several additional factors have been predicted to alter a female's mate acceptance threshold (Jennions & Petrie 1997), including differences in female condition; poorer condition females should be less discriminating. The trade-up hypothesis suggests that when females encounter potential mates sequentially, virgin females should have a low threshold to ensure fertilization, but may trade up to higher quality males in subsequent matings by using increasingly restrictive thresholds (Halliday

1983, Pitcher *et al.* 2003). Finally, mutual mate choice by both sexes appears to be widespread in insects (Bonduriansky 2001). When both sexes discriminate among potential mates, single sex optimization models are less applicable than dynamic game approaches (e.g. Parker 1983, Johnstone 1997).

In recognition system terminology (Reeve 1989), both male and female *Photinus* can be categorized as 'search-and-settle' evaluators, since both sexes can only accept a single mate per night. Both sexes also have opportunities to sample many potential mates. During each nightly flight period, males have the opportunity to sequentially assess several females, while stationary females can assess and differentially respond to multiple males that are signaling simultaneously in their vicinity. Prolonged courtship dialogs may even provide females with an opportunity to repeatedly assess the same male's signals in order to gain a more accurate assessment of male quality (Luttbeg 1996). In addition to these sex differences in sequential vs. simultaneous mate assessment, search costs are markedly asymmetrical. *Photinus* males not only incur higher energetic costs of flight and signaling, but also are differentially exposed to higher predation risk from spiders and bats (Lloyd 1973). Additionally, *Photinus* males are specifically targeted by predatory *Photuris* fireflies, whose females lure their prey by facultatively mimicking the flash responses produced by *Photinus* females (Lloyd 1979, 1997).

Integrating aspects of recognition and mate choice theory allows us to make several predictions concerning the context-dependence of mate acceptance thresholds in fireflies (Fig. 6). The acceptance thresholds of *Photinus* females are predicted to be more restrictive when operational sex ratios become more male-biased, and when either mean or variance in male quality (nuptial gift size) is higher. Additionally, temporal shifts in female thresholds are expected, such that females are predicted to be more restrictive early during the nightly mating period as well as earlier in the mating season. Finally, virgin females are predicted to be less discriminating than previously-mated females.

The acceptance thresholds for mate choice are similarly predicted to depend on operational



**Fig. 6.** Predicted determinants of mate acceptance thresholds for both sexes in *Photinus* fireflies (see text for explanation).

sex ratios, variance in female quality, and time remaining in the mating period and season. Furthermore, males with low residual reproductive value due to declining male resources for spermatophore production are predicted to have more restrictive thresholds. Finally, while males clearly bear the burden of mate search costs, predators differ in their predicted effects on acceptance thresholds; for most types of predators, increased predation will raise search costs and thus should lower mate acceptance thresholds. However, in the case of increased predation due to flash-mimicking *Photuris* females, males are predicted to raise their acceptance threshold to minimize fatal acceptance errors (Fig. 6).

Some of these predictions are supported by empirical evidence of shifts in mate acceptance thresholds during *Photinus* firefly courtship (Lewis & Wang 1991, Cratsley & Lewis 2004). Male choice, in which males selectively reject less fecund females after contact, appears mainly later during the mating season (Cratsley & Lewis 2004). This increase in males' acceptance thresholds may reflect an increase in fitness gain from choosiness as variance in females' remaining egg load increases. Alternatively, it is possible that as males' own reproductive resources decline, the discounting of future reproductive value relative to the current mating opportunity leads to higher mate acceptance thresholds. Females also exhibit predictable shifts in their accept-

ance thresholds. Early during each nightly flight period, female response rate (both to males as well as to simulated flashes) is low, but females become more responsive after males stop flying (S. M. Lewis unpubl. data). A related shift in acceptance thresholds occurs seasonally, with female response rate increasing as the operational sex ratio (availability of potential mates) declines (Lewis & Wang 1991, Cratsley & Lewis 2004). Both of these shifts toward more permissive female acceptance thresholds are consistent with model predictions of sequential mate choice involving finite mating periods (Real 1990). Relaxed female acceptance thresholds under these conditions may reflect the increased probability of lost mating opportunities (and associated loss of the fitness benefit provided by male nuptial gifts) for females with thresholds that are too restrictive. Female nutritional status may also influence female acceptance thresholds. In laboratory experiments, *P. ignitus* females that had mated or had been fed on artificial diet showed reduced response rates to a wide range of simulated male flashes (Cratsley & Lewis 2003). This supports the prediction that a female's own condition influences her mate acceptance threshold. Because so many of these factors covary in field populations (e.g. operational sex ratio, female reproductive status, and male quality variation), experimental manipulations will be required to separate their contributions to determining mate

choice thresholds. Some features of *Photinus* courtship have been recreated in a laboratory setting using tethered, flying males (Case 2004), which raises the possibility that laboratory as well as field experiments could be useful in studying these factors.

In conclusion, this review of firefly mate choice and recognition provides an integrated conceptual framework that considers both pre-copulatory and post-copulatory choice by each sex. *Photinus* females have been shown to distinguish among potential mates on the basis of their bioluminescent signals, with variation in male pulse rate and pulse duration demonstrated to be especially important. Female mate choice produces directional selection on male signal characters, in contrast to stabilizing selection expected to result from minimizing species recognition errors. Male mate choice also occurs in fireflies, with males rejecting low fecundity females. While recognition systems provide a useful framework for considering many kinds of discrimination behavior between dichotomous choices (desirable vs. undesirable cue-bearers, e.g. kin vs. non-kin, conspecific vs. heterospecific males), mate quality exhibits continuous variation, and mate choice models more successfully highlight several important factors determining conspecific mate acceptance thresholds. Mutual mate choice may characterize many mating systems, thus necessitating modeling approaches that incorporate choice by both sexes. Finally, it is clear that future theoretical and empirical work needs to integrate pre-copulatory mate choice with the many intersexual interactions that take place during and after copulation. Fireflies provide an excellent model system for studies of mate recognition and choice, and future experimental manipulations should shed light on the factors determining mate acceptance thresholds in both sexes.

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