

Nuptial Gifts and Sexual Selection in *Photinus* Fireflies¹

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SYNOPSIS. The phenomenon of nuptial gift transfer during mating occurs across a remarkably wide range of taxa, and such male donations are likely to influence both pre-copulatory and post-copulatory sexual selection. This paper reviews what is known about nuptial gifts in *Photinus* fireflies (Coleoptera: Lampyridae), and discusses the adaptive significance of spermatophores in firefly mating systems. During copulation *Photinus* males transfer a spiral, gelatinous spermatophore to the female: sperm are released into the female's spermatheca for storage, while the remainder of the spermatophore disintegrates within a specialized gland. Radiolabelling studies indicate that male-derived protein is used to help provision the female's developing oocytes, and multiply-mated females show increased fecundity. As most *Photinus* adults do not feed, these studies suggest that females should continue to forage for matings to supplement their diminishing larval reserves, even after they have gained sufficient sperm to fertilize their eggs. Male spermatophore mass declines across sequential matings, and smaller spermatophores are associated with lower paternity success in situations where males compete for fertilizations. Declining spermatophore size across sequential matings may thus lead to diminishing reproductive returns for firefly males. Taken together, these results suggest that seasonal changes in nuptial gift availability may contribute to reversals of traditional courtship roles, with male choice and female-female competition occurring as spermatophore availability declines.

INTRODUCTION

When Charles Darwin first conceived of sexual selection (Darwin, 1871), he envisioned differences in mating success that arise either through competition for access to mates or through mate choice. It has been recognized more recently that in many species where females mate with multiple males, postcopulatory processes can also contribute to sexual selection (Smith, 1984; Eberhard, 1996; Simmons, 2001). Post-copulatory sexual selection may arise either through competition among male gametes for access to fertilizations, a process known as sperm competition, or through preferential sperm use by females, a process known as cryptic female choice. All of these pre-copulatory and post-copulatory processes can interact to drive evolutionary changes in reproductive behavior, morphology, and physiology (Table 1).

During courtship and mating males of many diverse species provide females with nutritional contributions; these nuptial gifts can include captured prey, nutritional substances manufactured by male accessory glands, or various male body parts (reviewed by Boggs, 1995; Vahed, 1998). Male spermatophores, which consist of sperm packaged within a structure produced by male accessory glands, represent a type of nuptial gift found across a remarkably wide range of taxa (Mann, 1984). These male nutrient donations are likely to influence both pre-copulatory and post-copulatory sexual selection.

In this paper we review what is currently known about nuptial gifts in *Photinus* fireflies (Coleoptera:

Lampyridae), focusing on male spermatophore structure, transfer, and subsequent fate within females. We also examine the benefits accruing to females from male spermatophores, and discuss how the cost of spermatophore production may limit male mating opportunities. Most *Photinus* fireflies do not feed as adults (Williams, 1917; Lloyd, 1997). Reproduction is therefore based on resources acquired through larval feeding, so nuptial gifts may be of particular economic importance in this insect group.

Male nuptial gift production and transfer

Male spermatophore structure and transfer was described by van der Reijden *et al.* (1997) for *Photinus marginellus* and *P. ignitus*. The male reproductive system contains four pairs of accessory glands, the most prominent of which are the tightly coiled spiral accessory glands. These spiral glands manufacture the main structural spermatophore components, consisting of a spiral-shaped pre-spermatophore covered with two longitudinal rows of pyramidal scales. Three additional pairs of accessory glands are tubular and vary in length from the long (18–24 mm), medium (5–7 mm) to short (1 mm) accessory glands. During the early stages of copulation, secretions from these four male accessory glands are combined in the male ejaculatory duct with sperm that have been stored within the seminal vesicles. Within 1 hr, the resulting spirally coiled, gelatinous spermatophore (Fig. 1) has been transferred to the female. Male sperm are packaged into ring-shaped bundles within the anterior end of the spermatophore, and released into the female's sperm storage organ, the spermatheca. The remainder of the spermatophore enters a specialized structure within the female reproductive tract, the spermatophore-digesting gland, where the spermatophore disintegrates over the next few days.

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TABLE 1. Sexual selection can arise from either intersexual selection or intrasexual selection acting on two multiplicative reproductive fitness components: mating success (number of mates per lifetime), and fertilization success (proportion of fertilizations gained per mating).

	Mating Success	Fertilization Success
Intersexual selection	Mate choice	Sperm choice
Intrasexual selection	Mate competition	Sperm competition

Male spermatophore transfer during copulation occurs in many lampyrid species, including *Photinus aquilonius*, *P. greeni*, *P. pyralis*, and *P. obscurellus* (van der Reijden *et al.*, 1997), as well as in the diurnal firefly *Ellychnia corrusca* (Rooney and Lewis, 1999). In addition, based on the presence of either spermatophore remnants or male spiral accessory glands it seems likely that spermatophore transfer occurs in many other lampyrids, including *Pteroptyx valida* (Wing *et al.*, 1983), *Photinus macdermotti* (Wing, 1985), *Photinus carolinus*, and *Photuris sp.* (S.M.L., unpublished data).

Fate of spermatophores within females

Rooney and Lewis (1999) examined the fate of spermatophore-derived proteins using radiotracers. *P. ignitus* males were pre-mated to deplete their existing spermatophore and then injected with a ³H-labelled amino acid mixture. These labeled males were then allowed to mate with females that were later dissected at various timepoints post-mating. Radiolabel counts in each female’s spermatophore-digesting gland (SDG), mature oocytes, fat body, and other body tissues were determined by scintillation counting. In females dissected 3 hr after the beginning of copulation (0 day), the majority of label appeared in the SDG where the male spermatophore was located. However, radiolabel counts in the SDG declined over the next 2 day, while they showed a corresponding increase in female oocytes (Fig. 2). Very little radiolabel appeared in other female tissues, including the spermatheca, bursa copulatrix or the rest of the ovaries. These results indicate that *P. ignitus* females use male spermatophore protein to help provision their developing oocytes, and suggest that male nuptial gifts may be important supplements to female larval reserves for supporting female vitellogenesis.

Effects on female fecundity

The effect of receiving multiple spermatophores on reproductive output of *P. ignitus* females was examined by randomly assigning females to either a single mating or three consecutive matings with different males (Rooney and Lewis, 2002). Female fecundity (number of eggs laid) was significantly higher in triply-mated compared to singly-mated females (Fig. 3), but neither hatching success nor female longevity differed between mating treatments. Thus, male spermatophores in *P. ignitus* provide females with a direct

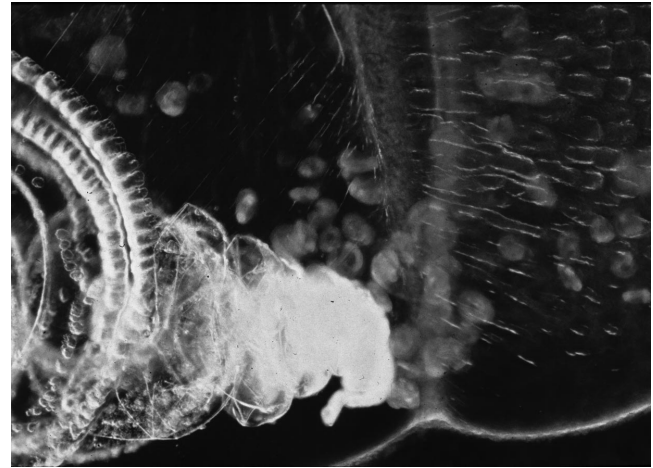


FIG. 1. Spiral spermatophore of a *P. ignitus* male inside the female reproductive tract. Rows of pyramidal scales are visible, and sperm rings are being released from the anterior tip of the spermatophore into the female’s spermatheca.

benefit measured in terms of increased fecundity. Nuptial gifts may be particularly important for female reproduction because larval energy reserves for non-feeding *Photinus* adults decline steadily. In addition, parasitoids might further deplete resources available for female reproduction. Field studies of *P. marginellus* showed that females were attacked by the dipteran parasitoid, *Apocephalus antennatus*, at higher rates than males and contained more parasitoid larvae per host (Lewis and Monchamp, 1994).

Costs and benefits to males

Spermatophore production appears to be costly to *Photinus* males. Cratsley *et al.* (2003) found that male

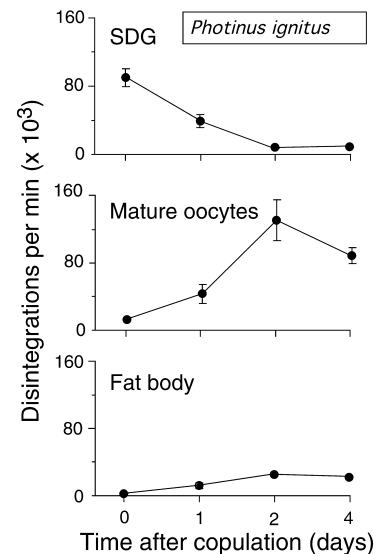


FIG. 2. Radiolabel counts (dpm × 10³, mean ± SE) in the spermatophore-digesting gland (SDG), oocytes, and fat body of *P. ignitus* females at various times following copulation with males injected with ³H-labelled amino acids (modified from Rooney and Lewis, 1999, permission from Behavioral Ecology).

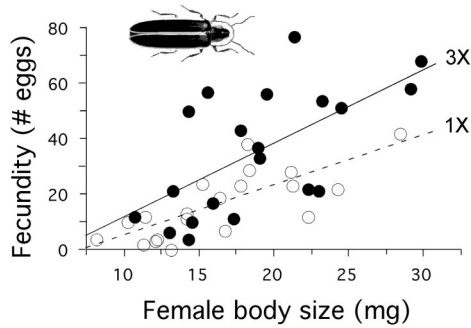


FIG. 3. Increase in fecundity of triply-mated *P. ignitus* females (solid circles and solid line) compared to singly-mated females (open circles and dashed line), corrected for variation in body weight (ANCOVA for mating effect, $F_{(1,66)} = 6.8$, $p = 0.01$; modified from Rooney and Lewis, 2002—Permission from Ecological Entomology).

spermatophore mass in *P. ignitus* declined across sequential matings (Fig. 4): there was an average decline of 75% between a male's first and fourth or subsequent spermatophore. In addition, the cost of spermatophore production may constrain male mating success; even when *Photinus* males were provided with access to receptive females every night, their mating success declined during the latter half of each male's adult lifespan. These limits on male spermatophore production are likely to alter nuptial gift availability as the mating season progresses, with seasonal declines in both the frequency and size of male spermatophores.

Larger spermatophores provide firefly males with a fitness benefit in terms of increased success when they compete with other males for fertilizations. Rooney (2000) manipulated the size of spermatophores transferred by *P. ignitus* males (based on the fact that recently-mated males produce smaller spermatophores), and then measured their subsequent paternity success using molecular markers. Smaller spermatophores resulted in lower paternity success when *P. ignitus* males were allowed to mate with previously mated females. This indicates that among those *Photinus* males that have successfully mated, the proportion of offspring they subsequently sire will vary with their spermatophore mass. Declining spermatophore size across sequential matings may thus lead to diminishing reproductive returns for firefly males.

CONCLUSION

It is clear that nuptial gifts have the potential to influence both pre-copulatory and post-copulatory aspects of firefly sexual selection in many ways (Cratsley, 2004; Cratsley and Lewis, 2003). For example, increased fecundity with multiple matings suggests that *Photinus* females should continue to forage for matings to supplement their own diminishing nutritional reserves, even after they have gained sufficient sperm to fertilize their eggs. Similarly, limits on male spermatophore production may cause seasonal changes in nuptial gift availability. Coupled with seasonal

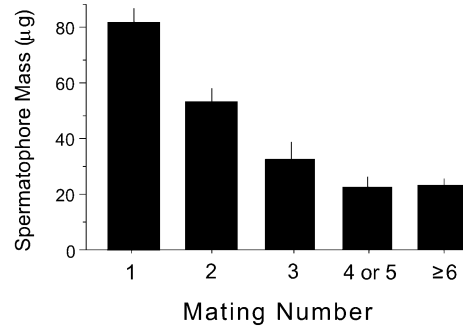


FIG. 4. Decrease in spermatophore size (dry weight, mean + 1 SE) across multiple matings by *P. ignitus* males (1st mating $n = 87$, 2nd $n = 34$, 3rd $n = 9$, 4th or 5th $n = 5$, $\geq 6^{\text{th}}$ $n = 7$). Modified from Cratsley *et al.* (2003), *Journal of Insect Behavior*.

changes in operational sex ratio that have been documented in *Photinus* (Lewis and Wang, 1991; C.K.C., unpublished data), these changes in nuptial gift availability have the potential to alter firefly courtship behavior. Early in the mating season, sex ratios are male-biased and most males readily produce spermatophores. This may result in male-male competition and female preference for males that can provide the largest nuptial gifts (Cratsley and Lewis, 2003). However, later in the season females outnumber males, and frequency and size of male spermatophores decline. As a result, male choice and female competition may become increasingly important. Although such a seasonal reversal in courtship behavior remains to be tested, examining the implications of nuptial gifts for firefly courtship and postcopulatory sexual selection should provide many fruitful avenues for future investigations.

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