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Differential allocation of male-derived nutrients in two lampyrid beetles with contrasting life-history characteristics

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Across diverse animal taxa, sperm is transferred from males to females during mating within a spermatophore produced by male accessory glands. In some insects, male spermatophores provide females with nutrients that may be used to increase reproductive output or for somatic maintenance, while in others no such benefits have been detected. Boggs suggested that variation in the current function of spermatophores may be explained by considering ecological and life-history factors. This study examined spermatophore function in *Ellychnia corrusca* and *Photinus ignitus* (Coleoptera: Lampyridae), two beetles that exhibit marked differences in adult diet, adult life span, and overwintering stage. During mating, males of both species transfer to females a complex, proteinaceous spermatophore, which is subsequently digested in a specialized sac within the female reproductive tract. Males of each species were injected with ^{3}H–radiolabeled amino acid mixtures and mated with conspecific females. The fate of spermatophore-derived proteins was determined by dissecting females at various times after mating with these radiolabeled males. Females of these two species showed markedly different patterns of incorporation of spermatophore-derived nutrients. *P. ignitus* females incorporated the majority (62%) of spermatophore-derived protein into maturing oocytes within 2 days after mating. In contrast, in *E. corrusca* a large percentage of radiolabel (46%) appeared in female fat body at 6 days after mating, with a threefold lower allocation to maturing oocytes compared to *P. ignitus*. These findings support the prediction that short-lived, nonfeeding females are selected to allocate a greater proportion of male-derived nutrients to reproduction, while longer-lived, feeding females are selected to allocate a greater proportion to somatic reserves and maintenance. These results suggest that life-history characteristics may be useful in explaining observed differences in spermatophore function across taxa. *Key words:* Ellychnia, firefly, life history, nuptial gifts, paternal investment, *Photinus,* radiotracer, spermatophore. *[Behav Ecol 10:97–104 (1999)]*

In numerous species, males provide females with nutritional contributions during courtship and copulation. Such nuptial gifts may include captured prey, nutritional substances produced by male accessory glands, or various male body parts (reviewed by Andersson, 1994; Thornhill, 1976; Thornhill and Alcock, 1983; Zeh and Smith, 1985). Spermatophores, consisting of sperm packaged within a structure produced by specialized male accessory glands, represent a common form of nuptial gift transferred during mating in diverse animal taxa (Mann, 1984). Male spermatophores have been shown in some insect species to provide nutritional benefits that increase female reproductive output (egg number or size) or contribute to female somatic maintenance, while such effects are lacking in other species (reviewed by Boggs, 1990, 1995; Gwynne 1997; Simmons and Parker, 1989; Vahed, 1998). Boggs (1990) developed a nutrient budget model to explain such variation in the relative influence of male-donated nutrients on female fitness components based on composition of adult diets and timing of female egg maturation. The examination of spermatophore function in closely related species with disparate life-history characteristics is likely to provide insight into selective factors responsible for the maintenance of male nuptial gifts.

During mating, males of several *Photinus* firefly species transfer a complex, protein-rich spermatophore to females (van der Reijden et al., 1997). After release of sperm bundles into the female spermatheca for storage, the spermatophore moves into a specialized compartment within the female reproductive tract, where it subsequently disintegrates. *P. marginellus* males fed rhodamine B (a fluorescent, thiol-reactive dye that covalently binds to proteins) transferred intensely fluorescent spermatophores to females during mating, and within 58 h female oocytes became strongly fluorescent. This work suggests that spermatophore-derived proteins or amino acids may be used by *Photinus* females to provision oocytes during vitellogenesis.

In this study we further investigated the current function of spermatophores in two lampyrid beetles, *P. ignitus* Fall and *Ellychnia corrusca* LeConte, which exhibit markedly different life histories. *Photinus ignitus* is a nocturnally active, bioluminescent firefly with short-lived, nonfeeding adults. *E. corrusca* is a diurnally active, nonluminescent beetle with long-lived, feeding adults that overwinter. We injected males of each species with a ^{3}H–labeled amino acid mixture, allowed them to mate with females, and determined subsequent rates and patterns of radiolabel incorporation into female tissues. We predicted that *P. ignitus* females would allocate spermatophore-derived proteins primarily to current reproductive output, due to their short adult life expectancy and lack of dietary protein sources for adults. In contrast, *E. corrusca* females were expected to show greater allocation toward female somatic maintenance and accumulation of metabolic reserves for overwintering.

METHODS

Ellychnia and *Photinus* include beetles that are extremely similar morphologically (LeConte, 1881), and McDermott (1964) classified these two genera in the same subfamily (Lampyrinae), tribe (Photinini), and subtribe (Photinina). However, these two lampyrid genera exhibit fundamental differences in

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several life-history characteristics. *P. ignitus* fireflies are nocturnally active and bioluminescent, and are distributed throughout the northeastern United States (Lloyd, 1966). In eastern Massachusetts adults form discrete breeding aggregations in open fields from late June to early August. *Photinus* beetles overwinter as subterranean larvae, feeding on earthworms and soft-bodied invertebrate prey (Hess, 1920; McDermott, 1964). Following adult emergence, males and females of most *Photinus* species are capable of mating multiple times, and females continuously mature and oviposit eggs throughout their 1- to 2-week adult life span (Buschman, 1977; Lewis and Monchamp, 1994; Lewis and Wang, 1991; van der Reijden et al., 1997; but see Wing, 1984). *Photinus* adults apparently do not feed at all (Williams, 1917; Wing, 1989), and thus adults rely on reserves stored from larval feeding for both somatic maintenance and reproduction.

Beetles in the *Ellychnia corrusca* species complex are common in forested areas across the eastern United States (Fender, 1970) and are diurnally active and nonluminescent. *Ellychnia* appear to rely on chemical signals for mate location (Lloyd, 1997). These beetles overwinter as adults (Williams, 1917), which have been observed feeding on maple sap and flowers in spring, and on aster and goldenrod in fall (Dillon and Dillon, 1972; Rooney and Lewis, personal observations). Both males and females can mate multiple times, and females continuously mature and oviposit eggs.

P. ignitus males and females were collected at night during their breeding season from June to August 1996 and 1997 in Lincoln, Massachusetts, USA. *E. corrusca* males and females were collected during the day during their breeding season from March to June 1997 in Lincoln and Belmont, Massachusetts. We examined rates and patterns of incorporation of spermatophore-derived proteins by mating radiolabeled *P. ignitus* and *E. corrusca* males to females and dissecting females at various times after mating. Before radiolabel injection, males were paired with females until mating occurred so that males would transfer their existing spermatophore and begin production of a new one. We separated these premating pairs approximately 2 h after the beginning of copulation; for both species, spermatophore transfer occurred within the first 90 min of copulation.

We injected premated males with 10 μCi of ^{3}H-labeled amino acid mixture (Amersham), and isolated them for 24 h to allow production of a new spermatophore. Although male spermatophores may also provide females with substances other than protein (Marshall, 1982), we focused on protein because it is a key nutrient limiting vitellogenesis (Wheeler, 1996). After 24 h males were placed with a different, field-collected female and allowed to mate. To determine the location of the transferred label, we interrupted copulations after approximately 3 h, separated pairs, and dissected females at various timepoints. *P. ignitus* females were dissected either immediately (0 days, $n = 6$ females), 1 day ($n = 4$), 2 days ($n = 6$), or 4 days ($n = 2$) after copulation ended; *E. corrusca* females were dissected at 0 days ($n = 3$), 2 days ($n = 4$), 4 days ($n = 5$), or 6 days ($n = 2$). Under 30× magnification, the following tissue categories were separately dissected out of each female: spermatophore-digesting gland (SDG), spermatheca (sperm storage organ), mature oocytes (defined as ≥600 μm diameter), ovaries (including immature oocytes and oviduct), bursa copulatrix, and all remaining somatic tissue. In a subset of females ($n = 11$ *P. ignitus*, $n = 14$ *E. corrusca*), fat body was separated from remaining somatic tissue and counted separately. Each tissue was placed in a 20 ml glass scintillation vial with up to 500 μl of tissue solubilizer (methanol : hydrochloric acid, 12:1), crushed with a glass rod, and solubilized overnight at 22°C. Scintillation fluid was added (5 ml Scintisafe, Fisher) and samples counted with a Packard Tricarb liquid scintillation counter. We converted measurements of counts per minute (cpm) to disintegrations per minute (dpm) using a standard 70% counting efficiency for tritium. No quenching was observed in preliminary tests using different tissue types or amounts (data not shown).

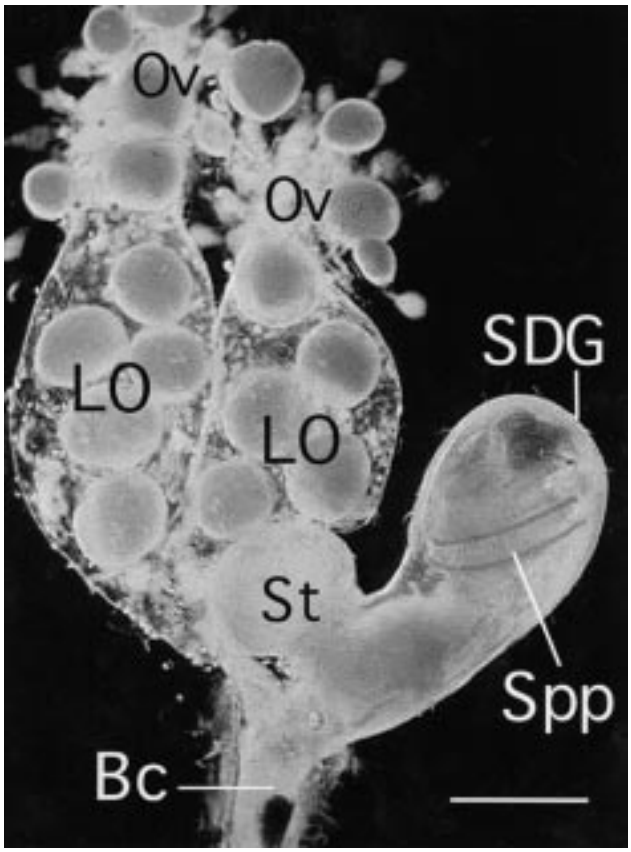

Figure 1
Reproductive tract of female *E. corrusca* 1 h after beginning of copulation (scale bar = 2 mm). Several mature oocytes are visible within the lateral oviducts (LO); oocytes in earlier stages of development are in terminal ovaries (Ov). Following deposition in the bursa copulatrix (Bc), sperm are stored within the spermatheca (St), while the male spermatophore (Spp) breaks down within the female spermatophore-digesting gland (SDG).

To compare different female tissues at various timepoints, we converted dpm for each sample to a percentage of the total label transferred to that female; this facilitated comparisons even when the total amount of radiolabel transferred varied among males. Patterns of allocation of male-derived protein were compared between *P. ignitus* and *E. corrusca* females using nonparametric Mann-Whitney tests due to heterogenous within-group variances.

RESULTS

E. corrusca male spermatophores were similar to those described previously for *Photinus marginellus* and *P. ignitus* (van der Reijden et al., 1997), consisting of a spirally coiled, gelatinous structure transferred to the female within 30 min after the beginning of copulation. After 1 h of copulation, sperm bundles had been released into the female spermatheca, and the remainder of the spermatophore, still largely intact, had moved into the spermatophore-digesting gland (SDG) (Figure 1). In both *E. corrusca* and *P. ignitus,* spermatophore transfer from injected males resulted in the transfer of a substantial amount of radiolabel to mated females; total counts

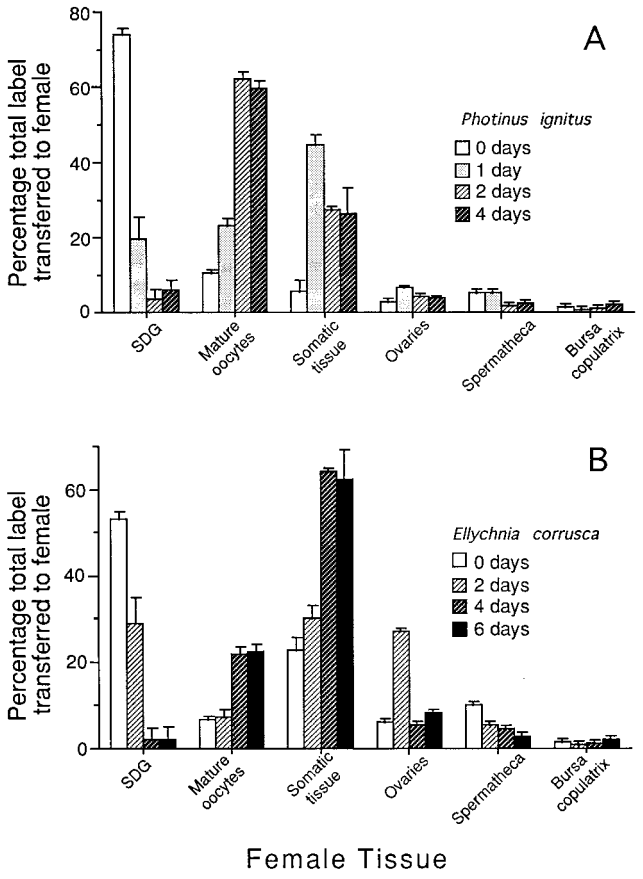

Figure 2
Distribution of radiolabel (as percentage of total label transferred, mean ± SE) in lampyrid females mated with males injected with ^{3}H-labeled amino acid mixture. (A) *Photinus ignitus* females dissected at 0 days (n = 6 females), 1 day (n = 4), 2 days (n = 6), and 4 days (n = 2) after mating and (B) *Ellychnia corrusca* females dissected at 0 days (n = 3), 2 days (n = 5), 4 days (n = 6), and 6 days (n = 2) after mating. Portions of female reproductive tracts counted separately were: spermatophore-digesting gland (SDG), mature oocytes (≥600 μm diameter), ovaries (including immature oocytes and lateral oviducts), spermatheca (including sperm), and bursa copulatrix. Somatic tissue refers to all remaining female tissue including the fat body.

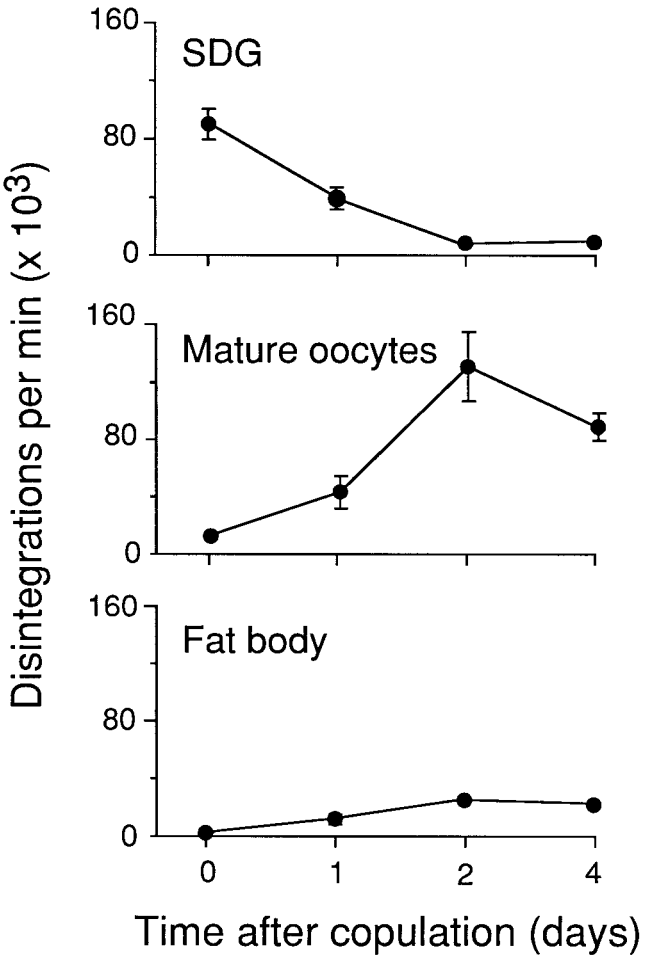

Figure 3
Radiolabel counts (dpm, mean ± SE) in female *P. ignitus* tissues dissected at various time points after mating with ^{3}H-labeled males.

in mated females ranged from 53,000 to 827,000 dpm in 14 *E. corrusca* females and from 80,000 to 390,000 dpm in 18 *P. ignitus* females.

In *P. ignitus* females dissected 3 h after the beginnning of copulation (0 days), 74% of the total radiolabel transferred was still associated with the spermatophore located within the female (Figure 2A). The next highest percentage of labeled male protein in *P. ignitus* females at 0 days was about 11% in mature oocytes located in the lateral or common oviducts. By 1 day after mating, SDG counts declined sharply as the spermatophore disintegrated, and the largest percentage of radiolabel, 44%, was found in female somatic tissue. By 2 days after mating, 62% of the total label transferred appeared in mature oocytes, with female somatic tissue accounting for an additional 27%. All remaining tissues of *P. ignitus* females, including ovaries, spermatheca (with sperm), and bursa copulatrix, each contained less than 10% of total label across all four time points. The redistribution in *P. ignitus* females of male-derived label from the SDG, where the spermatophore is initially deposited, to mature oocytes by 2 days after mating is apparent in radiolabel counts expressed as dpm over time after mating (Figure 3).

In *E. corrusca* females dissected 3 h after the beginnning of copulation (0 days), 53% of the total radiolabel transferred was present initially in the SDG (Figure 2B), with about 23% in female somatic tissue. As the spermatophore disintegrated within the SDG, a rapid decline in SDG counts was accompanied by a concomitant increase to 64% of radiolabel appearing in female somatic tissue at 4 days (Figure 2B). The majority of this somatic increase was due to increased counts in female fat body (Figure 4), which represented 15%, 37%, and 46% of the total radiolabel in *E. corrusca* females at 2, 4, and 6 days after mating, respectively. Radiolabel present in *E. corrusca* mature oocytes reached a maximum of 22% at 6 days after mating, and both the spermatheca and bursa copulatrix contained less than 10% of total label across all four time points.

Patterns of allocation of spermatophore-derived protein differed markedly between females of the two species. *P. ignitus* females showed a significantly higher percentage of radiolabeled protein in mature oocytes (mean ± SE = 62 ± 4.3% between 2 days and 4 days after mating, n = 8) compared to the percentage allocated to mature oocytes by *E. corrusca* females (22 ± 1.2% between 4 days and 6 days after mating, n = 7: Mann-Whitney U test, p = .001). This allocation difference was not due to any differences in female reproductive output, because numbers of mature oocytes were nearly iden-

Table 1
Review of previous insect studies examining the possible nutritional roles for male spermatophore

Species[a]	Label	Female tissue (% of total radiolabel transferred)	Peak incorporation (days after mating)	Effect on female
Lepidoptera				
Colias eurytheme[1,5]				
Alfalfa butterfly	^{3}H-arginine or leucine	Eggs = 36% Somatic = 20% (protein restricted diet)	Day 1 Day 1	↓ Spermatophore size = ↓ in oviposition rate and longevity
Danaus plexippus[2,3,4]				
Monarch butterfly	^{3}H-protein hydrolysate	Eggs = +	Day 9	↓ Spermatophore size = shorter refractory period, no effect on lifetime fecundity or longevity[3]; ↑ # of spermatophores = ↑ lifetime fecundity[3]; ↑ # of spermatophores = no effect on longevity, lifetime fecundity, fertility, or egg weight[4]
Dryas julia[6]		Eggs = +	Day 5	↓ Spermatophore size = shorter refractory period
Euphydryas editha and *E. chalcedona*[7]				
Checkerspot butterflies				↓ Spermatophore size = no effect on fecundity or fertility
Heliconius hecale[2]		Eggs = 14% Somatic = 34%	Day 3 Day 3	
Heliconius erato[2]		Eggs = +	Day 9	
Heliconius charitonius[6,7]		Eggs = +	Days 8 and 20	↑ # of matings = ↓ in female foraging time
Ostrinia nubilalis[8]				
European corn borer				↓ Spermatophore size = ↓ lifetime fecundity, no effect on oviposition rates, fertility, or longevity
Pieris napi[9]				
White cabbage butterfly				↓ Spermatophore size = ↓ lifetime fecundity ↓ Spermatophore size = ↓ longevity
Polygonis c-album[10]				
Comma butterfly	U-^{14}C protein hydrolysate	Eggs = 40%	Unknown	↓ Spermatophore size = ↓ amount of M and F proteins allocated to eggs
Trychoplasia ni[11]				
Cabbage looper moth				↑ # of spermatophores = ↑ lifetime fecundity and oviposition rate
Utethesia ornatrix[12]				
Arctiid moth				↑ # of spermatophores = ↑ lifetime fecundity, but no effect on longevity or egg mass
Orthoptera				
Blatella germanica[13]				
German cockroach	^{14}C-hypoxanthine	Eggs = 81% (low female dietary protein) Eggs = 24% (high female dietary protein)		
Chorthippus brunneus[14]				
Grasshopper	^{3}H-leucine	Eggs = + Somatic = +	Day 1 Day 1	↑ # of spermatophores (unrestricted diet) = ↑ oviposition rate, no effect on lifetime fecundity; ↑ # of spermatophores (restricted diet) = ↑ lifetime fecundity and oviposition rate

Table 1, continued

Species[a]	Label	Female tissue (% of total radiolabel transferred)	Peak incorporation (days after mating)	Effect on female
Decticus verrucivorus[15,16]				
Wartbiter	^{14}C-protein hydrolysate	Ovaries = 235% Immature eggs = 35% Mature eggs = 85%	Day 3–4 Day 5–8 Day >12	↑ in spermatophore # and size = no effect on lifetime fecundity or longevity
Gryllus bimaculatus[17]				
Field cricket				↑ # spermatophores = ↑ oviposition rate, egg mass, and fertility; no effect on longevity or lifetime fecundity
Melanoplus sanguinipes[18]				
Migratory grasshopper	^{3}H-leucine	Ovaries = 20% Hemolymph = +	Day 3 Day 1	↑ # of spermatophores = ↑ rate of egg production
Plebeiogryllus guttiventris[19]				
Cricket				↑ # of spermatophores (normal food) = ↑ lifetime fecundity; ↑ # of spermatophores (starvation) = ↑ lifetime fecundity and longevity
Poecilimon veluchianus[20]				
Buskcricket				↑ # of spermatophores = ↑ dry weight of larvae
Requena verticalis[21,22,23]				
Bushcricket	U-^{14}C protein hydrolysate	Eggs = 39% Somatic = 59% (ad lib diet) Eggs = 32% Somatic = 6% (limited diet)	Day 9–13 Day 9–13 Day 9–13 Day 9–13	↑ Spermatophylax size or number = ↑ egg size; ↑ spermatophylax number = ↑ lifetime fecundity
Xestoblatta hamata[24]				
Tropical rainforest cockroach	^{14}C-hypoxanthine	Eggs = 29% (no female dietary protein) Eggs = 15% (high female dietary protein)	1st ootheca 1st ootheca	↓ Uric acid (similar to spermatophore) = ↓ rate of oviposition
Coleoptera				
Acanthosecelides obtectus[25]				
Bean weevil	^{14}C-arginine or histidine	Eggs = + Hemolymph = +	Day 1–2 Day 2	↑ # of spermatophores = ↑ Oviposition rate
Caryedon serratus[26]	^{35}S-methionine	Eggs = + Hemolymph = +	Day 1 Day 6	↑ of spermatophores (in both restricted and unrestricted diets) = ↑ Oviposition rate, ↑ lifetime fecundity
Ellychnia corrusca[27]				
Lampyrid beetle		Eggs = 22% Fat body = 46%	Day 6 Day 6	
Photinus ignitus[27]				
Lampyrid beetle		Eggs = 62% Fat body = 5%	Day 2 Day 4	

For radiolabeling experiments (all were performed with ^{3}H or ^{14}C-labeled amino acid mixtures unless otherwise noted), percentages were calculated using the maximum amount of label found in particular tissues over the time course divided by estimated total amount of label transferred to the females with the spermatophore (where percentages could not be calculated from the original data presented, presence of label is indicated as +). Also included are effects of spermatophore size (experimentally manipulated by varying male mating history) or spermatophore number (comparing multiply mated females to singly mated females) on female longevity or reproductive output.

[a] References: 1, Boggs and Watt, 1981; 2, Boggs and Gilbert, 1979; 3, Oberhauser, 1989; 4, Svard and Wiklund, 1989; 5, Rutowski et al., 1987; 6, Boggs, 1981; 7, Jones et al., 1986; 8, Royer and McNeil, 1993; 9, Wiklund et al., 1998; 10, Wedell, 1996; 11, Ward and Landolt, 1995; 12, LaMunyon, 1997; 13, Mullins and Keil, 1980; 14, Butlin et al., 1987; 15, Wedell and Arak, 1989; 16, Wedell, 1993; 17, Simmons, 1988; 18, Freidel and Gillott, 1977; 19, Bentur and Mathad, 1980; 20, Reinhold and Heller, 1993; 21, Gwynne and Brown, 1993; 22, Gwynne, 1984; 23, Gwynne, 1988; 24, Schal and Bell, 1982; 25, Huignard, 1983; 26, Boucher and Huignard, 1987; 27, this study.

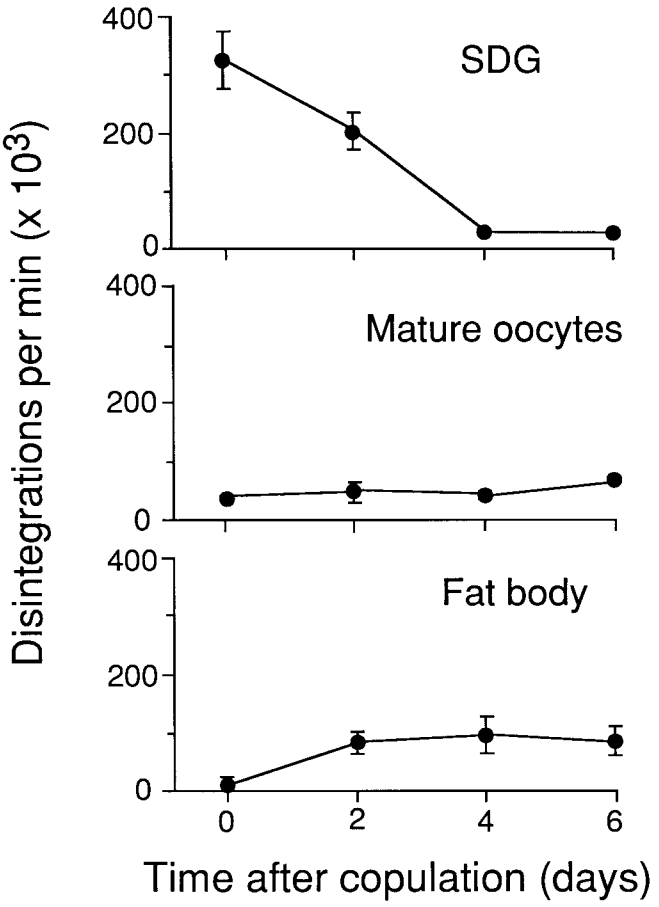

Figure 4
Radiolabel counts (dpm, mean ± SE) in female *E. corrusca* tissues dissected at various time points after mating with ^{3}H-labeled males.

tical between the two species (*P. ignitus*: 24 ± 3.0 mature oocytes, $n = 19$ females; *E. corrusca*: 28 ± 4.3 mature oocytes, $n = 14$; $t = 0.74$, $p = .47$). *E. corrusca* females, on the other hand, showed significantly greater allocation to fat body at 2 and 4 days after mating (27 ± 4.0%, $n = 9$ females) compared to *P. ignitus* females at 1, 2, and 4 days after mating (4 ± 0.3%, $n = 8$ females; Mann-Whitney U test, $p = .001$).

DISCUSSION

This study demonstrates that both *P. ignitus* and *E. corrusca* males produce and transfer a protein-rich spermatophore to females during mating, but that females from these two lampyrid species exhibit markedly different allocation patterns of radiolabeled protein derived from these male spermatophores. *P. ignitus* females allocate spermatophore-derived protein primarily to maturing oocytes, whereas the majority of male-derived protein is allocated to fat body reserves by *E. corrusca* females.

Three major hypotheses concerning the current adaptive significance of spermatophores have been proposed (reviewed by Boggs, 1995; Gwynne, 1997; Simmons and Parker, 1989; Thornhill and Alcock, 1983; Vahed, 1998; Wedell, 1993): (1) protecting the male's ejaculate to ensure successful or increased sperm transfer, (2) providing nutritional contributions that enhance female fecundity or survival *without* increasing male paternity, and (3) providing nutritional contributions that increase the number or viability of offspring sired by the contributing male.

Previous studies examining possible nutritional roles for male spermatophores in insects are summarized in Table 1. These studies fall into two main categories, the first consisting of studies in which males were fed or injected with specific radiolabeled compounds and the fate and rate of allocation of male-derived nutrients within mated females subsequently determined. Many of these radiotracer studies have demonstrated transfer of substantial amounts of male-derived nutrients to oocytes, supporting a direct trophic role for male spermatophores. Similarly high levels of allocation of male-derived protein to mature oocytes as demonstrated here for *P. ignitus* females have been found in the orthopteran *Decticus verrucivorus* (Wedell, 1993), although peak incorporation into oocytes occurs considerably more rapidly in *P. ignitus* (2 days versus >12 days). In two cockroaches, *Blattella germanica* and *Xestoblatta namata,* a large percentage (up to 81%) of the urates transferred along with spermatophores are incorporated into developing oocytes and have been suggested to provide an energy source during embryogenesis (Mullins and Kiel, 1980; Schal and Bell, 1982).

Other studies have explored possible nutritional roles for insect spermatophores by manipulating experimentally either the number or size of spermatophores received by females and measuring effects on female reproductive output or longevity (Table 1; also reviewed by Boggs, 1995). For many species, increasing either male spermatophore size or number results in increased female fecundity (egg number, egg size, or oviposition rate) or longevity, although a few species show no effect of male spermatophores on either female fecundity or longevity. Additionally, several studies have demonstrated an increase in female fecundity with multiple matings only when females are given low-protein diets (Table 1). Thus, two lines of evidence support the idea that spermatophores in certain insects currently function as a male nutritional contribution that increases availability of protein for vitellogenesis: (1) radiolabeling studies that demonstrate allocation of substantial amounts of spermatophore-derived protein to oocytes, and (2) dependence of spermatophore effects on female dietary protein. However, it is also possible that increased female fecundity with multiple matings or larger spermatophores may in some cases involve endocrine effects of fecundity-enhancing substances produced by male accessory glands (reviewed by Gillott, 1988; Leopold, 1976).

Few studies have attempted to identify selective forces responsible for the differences in male spermatophore function observed among species. Boggs (1990) suggested that differences in adult diet and temporal patterns of female vitellogenesis may generate differences in the relative importance of male-derived nutrients to female reproduction. The present study further suggests that life-history differences may help explain observed interspecific differences in male spermatophore function. The difference in allocation of male-derived nutrients observed between these two lampyrid beetles is consistent with their divergent life histories. Our findings suggest that in *P. ignitus,* male spermatophores represent nutritional contributions that increase female reproductive output, consistent with Boggs's (1990) prediction of an increased nutritional role for male spermatophores in species lacking adult dietary protein sources. *P. ignitus* adults do not feed, and because female vitellogenesis is a nutrient-limited process (Wheeler, 1996), female reproductive output in the absense of spermatophore-derived nutrients must depend entirely on resources acquired from larval feeding. Thus, nutrients available in male spermatophores are likely to be crucial for *P. ignitus* female reproduction. In addition, their short 1- to 2-week adult life span may limit any possible benefit that *P. ignitus* females could gain from allocating nu-

trients to storage for either future maintenance or reproduction. These life-history features may have been involved in selection for the ability of *P. ignitus* females to rapidly divert the majority of spermatophore-derived proteins to maturing oocytes, thus maximizing current reproductive output. The transient increase in radiolabel observed in somatic tissue of *P. ignitus* females likely represents radiolabeled polypeptides or amino acids being transported in the hemolymph between the SDG, fat body, and ovaries; similarly high initial hemolymph counts that decline over about 24 h have been found in other radiotracer studies (Boucher and Huignard, 1987; Friedel and Gillot, 1977; Huignard, 1983). In *P. ignitus* we cannot currently distinguish whether male-derived nutrients are allocated to eggs fertilized by the donating male or by other males.

In contrast, *E. corrusca* females allocate the majority of male-derived proteins to fat body. This allocation may represent long-term storage, as radiolabel counts remained high in female fat body over at least 6 days after mating. Reduced allocation of male-derived nutrients to reproduction in *E. corrusca* females, which feed as adults, compared to that shown by nonfeeding *P. ignitus* females agrees with the prediction of Boggs' (1990) model based on adult diet, but other life-history characteristics may also contribute to selection for these differing allocation patterns. Unlike *Photinus, E. corrusca* adults live for several months and overwinter in the adult stage. The large metabolic cost associated with overwintering leads to the accumulation of extensive fat body reserves before diapause (Leather et al., 1993). *E. corrusca* females collected in the fall have greatly increased fat body volume compared to females collected in the spring (Rooney J, personal observation). Adult overwintering, combined with availability of alternative protein sources in the adult diet, may have resulted in selection for *E. corrusca* females to allocate male-derived protein to long-term storage to support the metabolic demands of overwintering.

Although not addressed in this study, it is also possible that defensive compounds may be transferred to the female in the male spermatophore. Lampyrid beetles contain defensive steroidal pyrones called lucibufagins, which are deterrent to predatory spiders and thrushes (Eisner et al., 1978, 1997). Several coleopteran and lepidopteran species are known to transfer defensive compounds during mating (Eisner et al., 1996; LaMunyon, 1997; Sierra et al., 1976). Additional comparative studies of species with different life histories will provide further insight into spermatophore evolution.

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