Energy and Predation Costs of Firefly Courtship Signals

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ABSTRACT: Animal courtship signals include many highly conspicuous traits and behaviors, and it is generally assumed that such signals must balance the benefits of attracting mates against some fitness costs. However, few studies have assessed the multiple costs potentially incurred by any one courtship signal, so we have limited understanding of the relative importance of different costs. This study provides the first comprehensive assessment of signal costs for *Photinus* fireflies (Coleoptera: Lampyridae), using controlled experiments to measure both the energy and predation costs associated with their bioluminescent courtship signals. We measured energy required to generate bioluminescent flashes, using differential open-flow respirometry, and found that flash signaling results in only a nominal increase in energy expenditure above resting levels. These results suggest that the energy required to generate bioluminescent flashes represents a minor component of the total cost of firefly courtship. However, controlled field experiments revealed that visually oriented predators imposed major costs on firefly courtship signals, with higher signaling rates significantly increasing the likelihood of predation. Together with previous results demonstrating that female fireflies prefer more conspicuous courtship signals, these results support the importance of multiple-receiver communication networks in driving signal evolution.

Keywords: bioluminescence, communication networks, Lampyridae, sexual selection, signaling.

Mate choice in many animals favors those individuals exhibiting the most conspicuous visual, acoustic, or olfactory

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signals (Andersson 1994). Signal costs play a critical role in sexual selection theory because they are required to prevent the runaway evolution of exaggerated courtship signals as well as to maintain signal reliability (Grafen 1990; Maynard Smith and Harper 2003). Signal costs could arise through diverse mechanisms, including immediate reductions in signalers' fitness through parasitism or predation (Cade 1975; Tuttle and Ryan 1981; Zuk and Kolluru 1998) or indirect fitness reductions caused by heightened energy expenditure. However, few studies have quantitatively assessed the multiple costs that might be incurred by courtship signals (Kotiaho 2001). Even among the well-studied acoustical signals produced by arthropods and amphibians, most studies have focused on either energy or predation costs (e.g., Cade 1975; Prestwich et al. 1989; Zuk et al. 1995). Indeed, multiple costs have been measured in only a few species (Tuttle and Ryan 1981; Bucher et al. 1982; Kotiaho et al. 1998), making it difficult to determine the relative importance of different cost categories.

Bioluminescent signals are used by diverse organisms, including numerous arthropods, polychaetes, mollusks, and fishes (Wilson and Hastings 1998; Herring 2000). Surprisingly, however, the costs associated with bioluminescence have not been quantified. In *Photinus* fireflies, courtship relies on rhythmic, precisely timed bioluminescent flashes that are emitted by a light-producing lantern located on ventral abdominal segments (Lloyd 1966; Carlson and Copeland 1985). Male *Photinus* fireflies emit bioluminescent signals in two courtship contexts. Males signal as they fly in search of females; once a female responds, males generally land and engage in a lengthy courtship dialogue with females (Vencl and Carlson 1998; Demary et al. 2006). Within *Photinus* species, males vary in the pulse duration and pulse rate of their courtship signals, with coefficients of variation ranging from 10% to 20% for flash timing parameters; females prefer signals with longer flash durations or faster flash rates when choosing their mates (Branham and Greenfield 1996; Cratsley and Lewis 2003; Michaelidis et al. 2006).

Sexual selection theory predicts that firefly mating signals are prevented from becoming increasingly conspicuous because they incur some unknown fitness costs, perhaps in the form of increased energy expenditure or

predation risk. The biochemistry of firefly bioluminescence has been extensively characterized and involves adenosine triphosphate–dependent production of a high-energy luciferin intermediate followed by oxygen-mediated degradation that results in rapid, highly efficient light production (Wilson and Hastings 1998). Recent work indicates that nitric oxide produced in the firefly lantern in response to neurotransmitter release controls oxygen access to photocytes by reversibly inhibiting mitochondrial respiration (Trimmer et al. 2001). However, the energy expenditure directly associated with bouts of flashing has not been measured.

In addition to energy costs, the courtship signals of *Photinus* fireflies have the potential to increase predation risk. Although bioluminescence in many fireflies appears to serve as an aposematic warning signal that deters generalist predators (reviewed by Lewis and Cratsley 2008), adults of *Photinus* fireflies remain vulnerable to specialist predators. *Photinus* populations throughout North and South America broadly overlap with predatory *Photuris* fireflies, which hunt and consume the smaller-bodied *Photinus* (Lloyd 1965, 1997; Nelson et al. 1975). Previous work has described the aggressive mimicry behavior shown by *Photuris* "femmes fatales," which attract *Photinus* males by mimicking the flash responses produced by prey females. In addition, Lloyd and Wing (1983) described *Photuris* attacks on aerial decoys containing light-emitting diodes (LEDs) that glowed or flashed continuously. Surprisingly, in spite of these detailed descriptions of *Photuris-Photinus* interactions, the predation costs of firefly signaling have not been experimentally quantified. Furthermore, no studies using controlled experiments have examined how natural variation in firefly courtship signals might affect the likelihood of predation.

In this study, we conducted separate laboratory and field experiments to examine possible energy and predation costs associated with the bioluminescent courtship signals of *Photinus* fireflies. Using differential open-flow respirometry, we examined the energy expenditure of individual fireflies during periods when they were flashing and periods when they were quiescent. We also investigated the possibility that maintaining bioluminescent capability might be energetically costly by comparing resting metabolic rates between nocturnal, bioluminescent fireflies and diurnal, nonbioluminescent lampyrid species. Finally, in field experiments, we quantified the predation costs of *Photinus* flash signals by measuring predator attraction to simulated *Photinus* courtship signals and comparing it with predator attraction to nonflashing controls, and we investigated how different *Photinus* signaling rates affected predation risk.

Material and Methods

Energetic Cost of Flash Production

The energetic cost of flashing was measured using *Photinus greeni* and *Photinus obscurellus* fireflies collected in Lincoln, Massachusetts (42°26′N, 71°18′W). Additionally, adults of two diurnally active, nonluminescent lampyrids, *Ellychnia corrusca* and *Lucidota atra*, were collected for comparison of their basal metabolic rates. All beetles were maintained individually on a reversed 16L : 8D light cycle in ventilated plastic cups with moist paper towels. Beetles were weighed to the nearest 0.1 mg immediately before and after respirometry measurements, and the mean of the two body mass values was used in calculations.

Carbon dioxide production by individual fireflies was measured by differential open-flow respirometry using a Li-Cor 6262 CO_2/H_2O analyzer (Li-Cor, Lincoln, NE) calibrated with a gravimetric mixture (Scott Specialty Gases, Plumsteadville, PA) and re-zeroed between measurements. Flow rates of 25- or 50-cm^3 min^{-1} were maintained by a Sable Systems mass flow control system (Sable Systems, Henderson, NV) through 23- or 72-cm^3 glass chambers; because of their larger body sizes, *Ellychnia* and *Lucidota* sp. were measured in the larger chambers (and at the higher flow rate) to allow unconfined movement. Because chamber temperatures ranged between 20° and 27°C, CO_2 data were corrected to 25°C assuming a Q_{10} of 2.5; actual Q_{10} was 2.59 ± 0.23 (mean ± SE, $n = 7$ individuals) between 20° and 25°C and 1.82 ± 0.12 between 25° and 30°C. The CO_2 levels were analyzed using Sable Systems Datacan V software and converted to microwatts assuming a respiratory quotient of 0.71 (27.7 kJ $L_{CO_2}^{-1}$).

During respirometry measurements, ethograms of each beetle's flash behavior (number of flash pulses) and walking behavior (presence/absence) were recorded in real time and subsequently verified from continuous video recordings of movement and flash behavior (Sony DCR-HC21 videorecorder). Natural flash signaling was elicited using flashing individuals of the same species placed nearby in transparent containers or by LEDs that simulated male flash signals. Most measurement periods were 30 min but were sometimes extended to 60 min to include adequate periods of each behavior. Behavioral observations were time-synchronized with respirometry data, taking into account washout and time lag properties of the respirometry system as determined by bolus injection. Metabolic rate calculations were based on periods during which beetles were observed either resting (without flashing or motion), flashing only, or walking only; periods with combined walking and flashing were not used for analysis. Flashing and nonflashing data are reported here only for individuals that displayed both behaviors on the same day, to minimize changes in body mass or age-related effects on metabolic

rates. To examine whether relative metabolic rate changed as a function of signaling rate (number of light pulses per min), we used data from *Photinus* females taken during periods of flashing (these females averaged 53 light pulses over 9.6 min).

Predation Cost of Firefly Signals

Field experiments to quantify the predation costs associated with bioluminescent courtship signals were conducted over nine nights between June 30 and July 26, 2005, at a field site in Lincoln, Massachusetts. At this site, a single species in the predatory *Photuris versicolor* complex and several *Photinus* prey species (*P. greeni, P. ignitus, P. obscurellus*) were active.

We used battery-powered microprocessors to drive 565-nm LEDs (Lampyridae Lures, Firefly Magic, Apple Valley, CA) that were programmed to accurately simulate the typical mating signals produced by *P. greeni* males (paired 100-ms pulses separated by a 1,200-ms interpulse interval). Each experimental unit had four wires (2-m length) leading to four LEDs that were programmed to repeat this simulated flash pattern at intervals of either 5, 6, 7, or 8 sec. Each night, four units were each deployed in a 3-m-diameter circular array where four LEDs were interspersed with four nonflashing controls (fig. 1*a*; when placed in the field, these units were visually isolated from one another). To monitor any predatory *Photuris* that were attracted, we constructed traps using 5-cm-diameter plastic capsules coated inside with Tangle-Trap paste (TangleFoot, Grand Rapids, MI); nonflashing control traps consisted of empty capsules similarly coated with Tangle-Trap (fig. 1*b*). Traps were deployed ∼0.5 m from the ground, supported individually by wire stakes. Arrays were placed in the field each evening by 2030 hours and were collected the following morning; because we were interested in the potential for *Photuris* predators to drive prey signal evolution, we presented prey signals during the entire activity period of these predators.

We measured the number and recorded the sex of any *Photuris* predators attracted to each LED-containing trap and each control trap. Here we report the number of capsules containing any predators, a conservative approach that accounts for the possibility that once a single predator had been caught, subsequent predators might be attracted by its flashing as well as by simulated *Photinus* mating signals.

To quantify predation risk due to bioluminescent signaling, we compared the number of LED versus control traps that attracted any predators using a paired *t*-test to match the four LED-containing traps to the four control traps within each array. To determine how flash signal intervals affected the likelihood of predation, we used only data from the LED traps and conducted a logistic regression analysis that modeled predator attraction as a binary response variable dependent on signal interval (flash patterns repeated at 5-, 6-, 7-, or 8-s intervals). For a video that illustrates firefly courtship signals and provides additional detail on methods and material, see the appendix in the online edition of the *American Naturalist*.
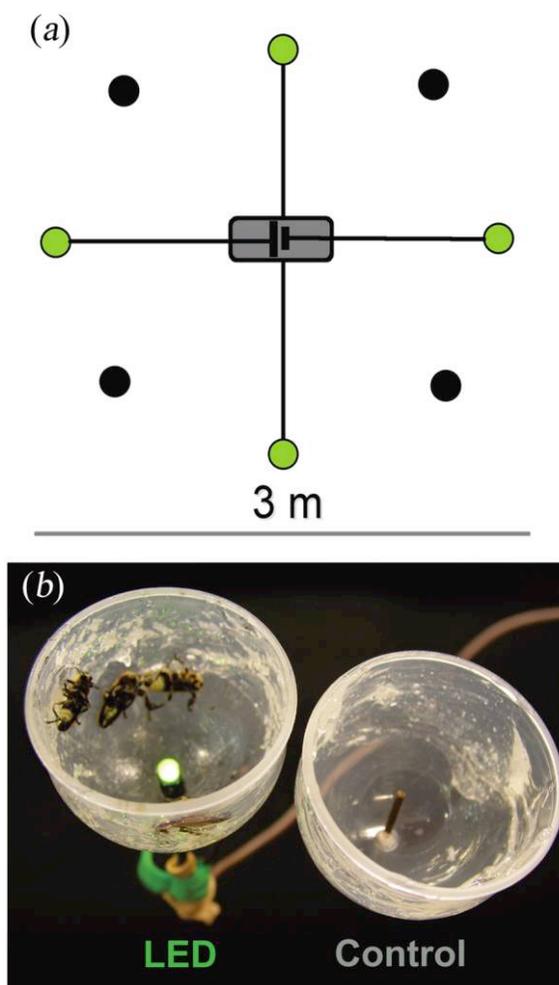

Figure 1: *a*, Schematic of experimental field array used to measure predation costs of firefly courtship signals. Each circular array included four traps (*green circles*) that contained light-emitting diodes (LEDs) designed to deliver flashes that simulated *Photinus greeni* mating signals (peak emission 565 nm; flash pattern consisting of paired 100-ms pulses separated by 1,200-ms interpulse interval); these were interspersed with four control traps lacking LEDs (*black circles*). *b*, Close-up illustrating LED-containing trap (*left*, shown with three captured *Photuris* predators) and control trap (*right*); interior surfaces of both were coated with Tangle-Trap.
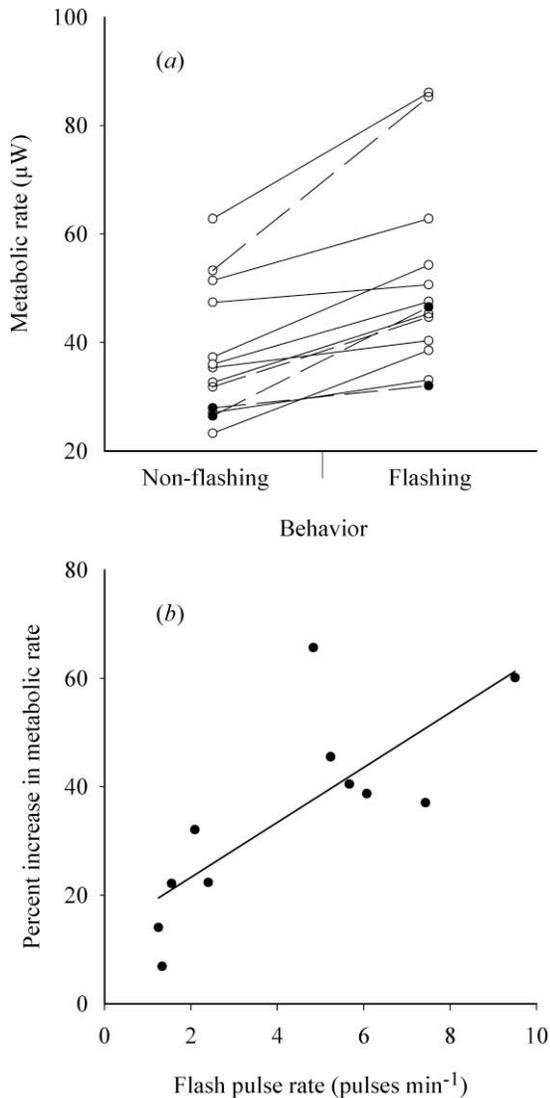
$t = 5.83$, df $= 12$, $P < .0001$), with an increase in metabolic rate during flashing averaging 37% $\pm$ 6% (± 1 SE, $n = 13$). However, the increased energy expenditure associated with flashing was below the 57% $\pm$ 12% increase above resting that was measured when fireflies were walking but not flashing (data not shown; paired $t = 5.14$, df $= 18$, $P < .0001$). In addition, percent elevation of metabolic rates above resting increased linearly with faster bioluminescent pulse rates during each measurement period (fig. 2*b*; regression $r^2 = 0.60$, $F = 13.47$, df $= 1, 10$, $P < .01$). Because maintaining bioluminescent capability in general might also have the potential to incur energy costs, we compared resting metabolic rates between nocturnal lampyrids capable of bioluminescence (but not flashing) and two diurnal, nonbioluminescent lampyrid species, *Ellychnia corrusca* and *Lucidota atra* (fig. 3). After controlling for differences in body mass (ANCOVA $F = 17.93$, df $= 1, 34$, $P < .0005$), we found no significant difference in resting metabolic rates between these bioluminescent and nonbioluminescent lampyrids ($F = 2.605$, df $= 1, 34$, $P = .116$).

In field experiments to assess predation costs associated with *Photinus* courtship signals, predatory *Photuris* fireflies were attracted significantly more often to LED-containing traps that emitted simulated courtship signals typical of *P. greeni* males than they were to control traps (fig. 4*a*; paired $t = 12.04$, df $= 30$, $P < .0001$). A comparison of the total number of *Photuris* predators attracted across all 31 experimental arrays revealed that 218 predators were attracted to traps with simulated courtship signals, while only four predators were attracted to control traps; females comprised 96% of all attracted *Photuris*. The time interval between flash signals also altered predation risk (fig. 4*b*), with shorter signaling intervals significantly increasing the risk of *Photuris* predation (logistic regression likelihood ratio, $\chi^2 = 8.57$, $n = 31$, $P = .0034$).

Figure 2: Firefly metabolic expenditure during bioluminescent signaling. *a*, Energy expenditure of individual *Photinus* spp. fireflies, based on differential open-flow respirometry measuring carbon dioxide production during periods with and without flashing. For all beetles, both measurements were conducted on the same day, and calculated values were restricted to periods when beetles were motionless. Solid lines indicate paired data for *Photinus greeni*, and dashed lines indicate paired data for *Photinus obscurellus*; filled circles denote males, and open circles denote females. *b*, Percentage increase in metabolic rates during flashing (relative to measured resting rates) of *Photinus* spp. females as a function of flash pulse rate during each measurement period (linear regression $r^2 = 0.60$, $F = 13.47$, df $= 1, 10$, $P < .01$; metabolic rate percent increase $= 5.29 \times$ flash rate $+ 12.70$).

Results

Energy expenditure measured during periods of flash production was significantly higher than when the same fireflies were measured during periods of rest (fig. 2*a*; paired

Discussion

This study represents the first controlled experiment to quantify the predation risk associated with firefly courtship signals and to assess how natural variation in male signals alters this risk. Our results demonstrate that signals produced by *Photinus* males incur substantial predation costs from predatory *Photuris* fireflies, which act as illegitimate eavesdropping receivers. While animal communication is often viewed as a closed dyadic interchange between a signaler and a receiver (Maynard Smith and Harper 2003; Searcy and Nowicki 2005), this study contributes to a growing recognition that signaling takes place within communication networks that often include multiple receiver types (Johnstone 1998; McGregor 2005; Searcy and Nowicki 2005). This study finds that predators eavesdropping
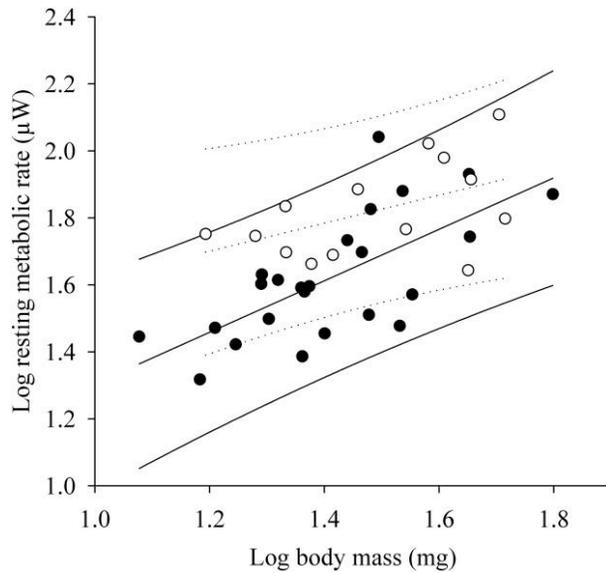
Figure 3: Comparison of resting metabolic rates between lampyrid beetles capable of bioluminescence (*solid symbols* and *solid lines*; $n = 24$: nine *Photinus obscurellus*, 14 *Photinus greeni*, one *Photuris* sp.) and diurnal, nonbioluminescent lampyrids (*open symbols* and *dotted lines*; $n = 14$: seven each for *Ellychnia corrusca* and *Lucidota atra*); curves represent 95% prediction intervals. A color version of this figure is available in the online edition of the *American Naturalist*.

on bioluminescent signals can impose major costs on mating signals, as shown in other signal modalities (Tuttle and Ryan 1981; Bucher et al. 1982; Zuk et al. 1995; reviewed by Verrell 1991; Zuk and Kolluru 1998; Kotiaho 2001).

Many other aspects of *Photuris-Photinus* interactions have been previously described. *Photinus* fireflies are chemically defended against many predators by steroidal pyrones (Eisner et al. 1978), yet they remain vulnerable to *Photuris* fireflies that sequester those compounds for their own defense (Eisner et al. 1997). The vast majority of *Photuris* predatory fireflies captured in our study were females, which are highly specialized predators known to actively hunt for and capture grounded males that are engaged in courtship dialogues with females (Lloyd 1965; Nelson et al. 1975; Lloyd and Wing 1983). Previous work on *Photinus* fireflies has also demonstrated that conspecific females prefer more conspicuous male courtship signals (reviewed by Lewis and Cratsley 2008), including longer flash durations and faster flash rates (Branham and Greenfield 1996; Cratsley and Lewis 2003; Michaelidis et al. 2006). Similar female preferences for more conspicuous male signals have been observed across many animal groups encompassing diverse signaling modalities (Reinhold et al. 1998; Greenfield 2002). In our study, higher flash signaling rates significantly increased the likelihood

of attack by predatory *Photuris* fireflies, which indicates strong viability selection against more conspicuous courtship signals. Thus, these results indicate that firefly courtship signals represent an evolutionary compromise between attracting mates and minimizing predation risk.

In contrast to high predation costs, we found that only relatively minor energy expenditure was required for fireflies to produce their bioluminescent flash signals. Compared with the 1.5- to 20-fold metabolic rate increases associated with the acoustic courtship signals of frogs, crickets, beetles (Prestwich 1994), and wax moths (Reinhold et al. 1998), the energy required by *Photinus* fireflies to produce their bioluminescent signals appears negligible, averaging only 37% above resting values and lower than the energy expense of firefly walking measured here. These energy expenditures are far below the energy requirements of any other arthropod signal that has been shown to reduce
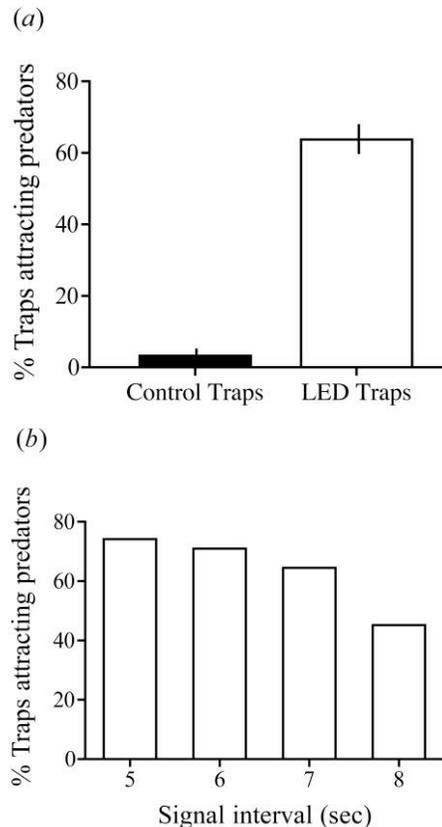

Figure 4: Predation costs of firefly courtship signaling. *a*, Mean percentage (± 1 SE) of control traps (*filled bar*) and LED-containing traps (*open bar*) that attracted any predatory *Photuris* fireflies (paired $t = 12.04$, df $= 30$, $P < .0001$). *b*, Effects of signal interval (simulated male courtship signals emitted at 5-, 6-, 7-, or 8-s intervals) on percentage of LED-containing traps that attracted any *Photuris* predators (logistic regression likelihood ratio, $\chi^2 = 8.57$, $n = 31$, $P = .0034$).

Table 1: Estimated energy budget for *Photinus* fireflies

Behavior	Metabolic rate (% increase above resting)	Estimated % of total energy budget
Flashing	37 ± 6	1.6–3.4
Walking	57 ± 12	1.2–2.5
Flying[a]	~1,900	19.5–42.5
Resting	0	46–73
Flying courtship[b] (flying and flashing)	~2,000	21.4–44.2
Walking courtship[b] (walking and flashing)	75	1.6–3.3

Note: Energy budget based upon courtship durations of 1–3 h night^{-1} (one-third while flying, two-thirds while walking); fireflies are assumed to be resting when not courting.

[a] Estimated from data for other insects (Bartholomew and Casey 1978; Kammer and Heinrich 1978), corrected for temperature assuming a Q_{10} of 2.5 (see text).

[b] Flashing contribution based on signaling rate of 20 pulses min^{-1} during flight and signaling rate of 1 pulse min^{-1} while walking. Calculations use the relationship in figure 2*b*.

fitness (Kotiaho et al. 1998). Additionally, energy expenditure from flashing is likely to make a relatively small contribution to the total energy budget of male *Photinus* fireflies (table 1). Flight undoubtedly requires much higher expenditure, although obtaining data under confinement for most insects during free flight is challenging at best and impracticable at worst. Estimates in table 1 are therefore based on existing data that compare hovering and resting metabolic rates for insects that will fly in confinement (Bartholomew and Casey 1978; Kammer and Heinrich 1978). This estimated energy budget for adult male fireflies suggests that most energy is expended while resting during the major portion of each day. The additional expenditure associated with bioluminescent signaling clearly contributes relatively little to the total cost of firefly courtship and to their total energy budget.

Although few other studies have measured these different types of signaling costs in the same organism (Kotiaho 2001), fundamental distinctions exist between energy and predation costs of signaling. Both are ideally measured in terms of how much they reduce signaler fitness, but only a handful of studies have actually demonstrated reduced survival or reproduction associated with energy expenditures of signaling (Kotiaho 2001). In contrast, direct and unambiguous fitness reductions occur when signals attract predators or parasitoids (Zuk and Kolluru 1998). Another key distinction lies in the effects such costs may have on evolutionary signal diversification. Signal energy costs are relatively invariant over space and time, while predation costs are likely to be highly variable due to spatial and temporal patterns of predator abundance. These differential predation costs will alter selection regimes across populations and may potentially lead to reproductive isolation and eventual speciation (Verrell 1991; Zuk and Kolluru 1998). Thus, local differences in natural selection on sexual signals via predation may have been a major force in firefly evolution (Lloyd 1997; Lewis and Cratsley 2008). *Photinus* fireflies occur in localized demes with relatively low dispersal capabilities, and only a subset of populations appears to overlap with signal-exploiting *Photuris* predators (Lloyd 1966). This has the potential to generate a geographic mosaic of selection on *Photinus* sexual signals, which could promote evolutionary diversification. The key role found here for eavesdropping natural enemies in firefly signaling systems demonstrates the importance of considering multiple receiver types within a communication network.

Acknowledgments

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