

1 The Canonical Firefly Luminosity Is Overestimated by
2 10^3 – 10^4 -Fold

3 David H. Silver^{1,*}

4 ¹Remiza AI

5 *Corresponding author: david@remiza.ai

6 ORCID: 0000-0002-3071-304X

7 **Abstract**

8 The luminous intensity of *Photinus pyralis* fireflies has been cited as 1/40 to 1/400 candlepower since the 1924 photometric study by Ives and Coblenz—a value corresponding to 9 3×10^{13} to 3×10^{14} photons per flash. We show that this canonical estimate exceeds the theoretical maximum imposed by luciferase abundance and quantum yield by 10^3 – 10^4 -fold. Direct 10 field measurements with a calibrated lux meter yield 10^{10} – 10^{11} photons per flash, consistent with 11 both our biochemical bound and independent reanalysis of historical and modern spectroscopic 12 data. The persistence of this error for a century reflects a disconnect between classical photometry 13 and modern bioluminescence research, the latter reporting light output almost exclusively 14 in arbitrary units rather than absolute photon flux.

15 **Keywords:** firefly bioluminescence; photometry; *Photinus pyralis*; luciferase

16 **1 Introduction**

17 The commonly cited value for firefly brightness—“1/40 candlepower”—traces to early twentieth- 18 century photometric studies by William Coblenz at the National Bureau of Standards. However, 19 examination of the original sources reveals two compounding errors that have persisted for over a 20 century.

21 Coblenz’s 1912 Carnegie Institution monograph reports that flash measurements for *Photinus* 22 *pyralis* ranged from “1/50 candle to 1/400 candle, the predominating values being 1/400 candle.”^[1] 23 The measurements were acknowledged as difficult: “Because of the inability to cause the insect to 24 flash rapidly for any length of time, the measurements were more difficult, and hence uncertain.” 25 Specimens varied in brightness depending on whether they were freshly caught or had been in 26 captivity; only about a dozen measurements were obtained from three healthy specimens. Despite 27 this acknowledged uncertainty, subsequent authors appear to have either misread “1/400” as “1/40” 28 (a transcription error) or cited the maximum value (1/50) while rounding to 1/40. The “1/40 29 candlepower” figure now appears in educational websites and textbooks, though Harvey’s treatise^[2] 30 correctly cites Coblenz’s range of “1/50 to 1/400 candle.”

31 The problem with this number becomes apparent when one considers the molecular machinery 32 responsible for firefly light production. The bioluminescent reaction is catalyzed by luciferase, 33 a 62-kDa oxygenase encoded by the *luc* gene, first cloned and sequenced in 1985.^[3] Luciferase 34 catalyzes the adenylation of D-luciferin by ATP to form a luciferyl-adenylate intermediate, which is 35 then oxidized by molecular oxygen to produce electronically excited oxyluciferin; relaxation to the 36 37

38 ground state emits a photon at approximately 560 nm.^[4] Because each catalytic cycle consumes
 39 one luciferin molecule and produces at most one photon, the total light output of a flash is bounded
 40 by the product of the number of luciferase molecules in the lantern, the number of turnovers per
 41 enzyme during the flash, and the quantum yield of the reaction.

42 Estimates from histological cell counts and biochemical assays place the luciferase content of the
 43 firefly lantern at approximately 10^{11} molecules—roughly 10^5 photocells, each containing 10^6 enzyme
 44 molecules at micromolar concentration.^[5,4] The quantum yield has been precisely measured at
 45 0.41, among the highest for any chemiluminescent system.^[6] Even under the most favorable kinetic
 46 assumptions, in which every enzyme molecule fires exactly once during the flash, the maximum
 47 possible output is 4×10^{10} photons—four orders of magnitude below the canonical value.

48 This discrepancy appears to have gone unnoticed for nearly a century because the two relevant
 49 literatures rarely intersected. Following the classical photometric studies of the early twentieth
 50 century, bioluminescence research shifted toward molecular biology and biochemistry, with light
 51 output reported almost universally in “arbitrary units” (a.u.) or “relative light units” (RLU) rather
 52 than absolute photon counts—a practice that persists in contemporary studies of firefly flash behav-
 53 ior,^[7,8] luciferase biochemistry,^[9,10] and bioluminescence spectroscopy.^[11] We undertook to resolve
 54 this puzzle by measuring firefly flash brightness directly with a calibrated lux meter, deriving the
 55 theoretical bound from first principles, and reanalyzing historical and modern datasets that can be
 56 converted to absolute photon flux.

57 2 Experimental

58 2.1 Theoretical framework

59 The total photon output of a firefly flash can be expressed as the product of five factors, each
 60 independently constrained by experiment (Table 1): the number of photocells N_{cells} (dimensionless
 61 count), the number of luciferase molecules per photocell N_{enz} (molecules/cell), the effective turnover
 62 rate k_{eff} (s^{-1}), the quantum yield Φ (photons/turnover, dimensionless), and the flash duration t (s).
 63 Under steady-state conditions, $k_{\text{eff}} \approx 0.01 \text{ s}^{-1}$ reflects oxygen-limited turnover *in vivo*.^[12,13] Under
 64 burst conditions, where the enzyme pool is pre-charged with substrate and discharged synchronously,
 65 each enzyme fires once ($n_{\text{turn}} = 1$). Three scenarios span the plausible range:

$$N_{\gamma}^{(\text{min})} = \underbrace{10^5}_{N_{\text{cells}}} \times \underbrace{10^6}_{N_{\text{enz}}} \times \underbrace{0.01}_{k_{\text{eff}}} \times \underbrace{0.41}_{\Phi} \times \underbrace{0.25}_{t} = 10^8 \text{ photons} \quad (1)$$

$$N_{\gamma}^{(\text{mid})} = 10^5 \times 10^6 \times 0.1 \times 0.41 \times 0.25 = 10^9 \text{ photons} \quad (2)$$

$$N_{\gamma}^{(\text{max})} = 10^5 \times 10^6 \times \underbrace{1}_{\text{burst}} \times 0.41 \times 1 = 4 \times 10^{10} \text{ photons} \quad (3)$$

66 2.2 Photometric units and conversions

67 Comparing historical and modern light measurements requires careful attention to units. Photo-
 68 metric units weight radiant power by human visual sensitivity, while radiometric units measure
 69 absolute power. Table 2 summarizes the key quantities.

70 The conversion between systems uses the luminous efficacy $K_m = 683 \text{ lm/W}$ at peak photopic
 71 sensitivity (555 nm) and the luminosity function $V(\lambda)$:

$$\Phi_e = \frac{\Phi_v}{K_m V(\lambda)}, \quad \dot{N} = \frac{\Phi_e}{E_{\gamma}} = \frac{\Phi_v \lambda}{K_m V(\lambda) hc} \quad (4)$$

Table 1: Biochemical parameters constraining firefly photon output. Each parameter is independently bounded; the product yields the theoretical photon range.

Parameter	Symbol	Min	Mid	Max	Constraint basis
Photocytes	N_{cells}	10^5	10^5	10^5	Histological counts in <i>P. pyralis</i> ^[5]
Enzymes/cell	N_{enz}	10^6	10^6	10^6	μM luciferase in photocytes ^[4]
Turnover (s ⁻¹)	k_{eff}	0.01	0.1	1	O ₂ -limited (min) to burst kinetics (max) ^[12]
Quantum yield	Φ	0.41	0.48	0.88	pH-dependent; 0.41–0.88 reported ^[6,4]
Duration (s)	t	0.25	0.25	1	Flash 200–300 ms; burst fires once ^[14]
Product	N_{γ}	10^8	10^9	4×10^{10}	Equations 1–3

Table 2: Photometric and radiometric quantities.

Quantity	Symbol	Unit	Definition
Radiant power	Φ_e	W	Energy per unit time
Photon rate	\dot{N}	s ⁻¹	Φ_e/E_{γ} where $E_{\gamma} = hc/\lambda$
Luminous intensity	I_v	cd	Power per solid angle, weighted by $V(\lambda)$
Luminous flux	Φ_v	lm	Total luminous power; $\Phi_v = 4\pi I_v$ (isotropic)
Illuminance	E	lux (lm/m ²)	Flux per unit area; $E = I_v/r^2$
Luminance	L	cd/m ²	Intensity per unit emitting area

For firefly emission at $\lambda = 560$ nm, $V(\lambda) \approx 0.995$ and $E_{\gamma} = 3.55 \times 10^{-19}$ J, so photometric and radiometric measures nearly coincide. One lux at 560 nm corresponds to 2.6×10^{12} photons·s⁻¹·m⁻².

The historical unit *candlepower* is approximately equal to one candela, but early standards (the “standard candle,” Hefner lamp, and Carcel lamp) differed by up to 10%, and one *lambert* equals $(1/\pi) \times 10^4$ cd/m².

2.3 Field measurements

Flash illuminance was measured in Sungai Petani, Kedah, Malaysia, in November 2025, using wild-caught fireflies (likely *Pteroptyx* species). A digital lux meter (0.1-lux resolution, ±4% accuracy, 2 Hz sampling) was positioned at 1–5 cm from the lantern of individually isolated fireflies in transparent containers. Ambient illumination was confirmed at 0.0 lux before each trial; a reference LED was measured nightly to verify instrument stability, and reported ∼4.2 lux before each measurement. Results are summarized in Table 3.

2.4 Photometric conversion

Illuminance E (lux) at distance r was converted to photon emission rate using:

$$\dot{N} = \frac{4\pi Er^2}{K_m V(\lambda) E_{\gamma}}$$

where $K_m = 683$ lm/W, $V(560 \text{ nm}) = 0.995$, and $E_{\gamma} = hc/\lambda = 3.55 \times 10^{-19}$ J. This formula assumes isotropic (4π sr) emission. However, firefly lanterns emit directionally: the photocycle

Table 3: Field lux-meter measurements (Sungai Petani, Malaysia, November 2025; $n = 5$ fireflies).

Distance	Mean Δ Lux	Max Δ Lux	Flashes
1 cm	0.30	0.5	10
2 cm	0.23	0.5	10
3 cm	0.04	0.2	10
4 cm	0.04	0.2	8
5 cm	0.03	0.2	10

layer sits beneath a dorsal reflector of uric acid crystals that backscatters upward-directed photons, channeling most light ventrally into a solid angle of approximately 1–2 sr (Figure 1).^[15] A geometric correction factor $f_{\text{geom}} = \Omega_{\text{eff}}/4\pi \approx 0.08\text{--}0.16$ was therefore applied.

2.5 Reanalysis of published data

Published measurements from Harvey & Stevens (1928)^[16] and Goh & Wang (2022)^[17] were converted to photon flux using the same photometric framework. Harvey & Stevens reported surface brightness of *Pyrophorus* click-beetle lanterns (0.045 lambert over $\sim 1 \text{ mm}^2$); Goh & Wang reported spectral irradiance of *Photinus* flashes measured by fiber-optic spectrometry.

3 Results

Peak flash illuminance ranged from 0.2 to 0.5 lux at 1–2 cm distance (Table 3), with weaker signals at greater distances following the expected inverse-square falloff. For the strongest flashes (0.5 lux at 1 cm), the isotropic calculation yields $\dot{N} \approx 10^{13}$ photons/s. Applying the geometric correction ($f_{\text{geom}} = 0.08\text{--}0.16$) and integrating over a 250-ms flash duration gives:

$$N_\gamma = 10^{10}\text{--}4 \times 10^{11} \text{ photons per flash}$$

This range is consistent with the theoretical bound ($10^8\text{--}4 \times 10^{10}$) and lies three to four orders of magnitude below the canonical 1924 value.

Two independent datasets corroborate this result (Table 4, Figure 2). Conversion of the Harvey & Stevens (1928) surface brightness measurement yields $\sim 6 \times 10^{11}$ photons per flash for the larger *Pyrophorus* lanterns. Goh et al. (2022) measured luminescent intensity of nine Taiwanese firefly species at 1.2–14 lux for males and 0.8–5.8 lux for females ($182\text{--}2048 \text{ nW/cm}^2$ and $123\text{--}850 \text{ nW/cm}^2$, respectively);^[17] assuming close-range measurement ($\sim 5 \text{ cm}$) and applying our photometric conversion with geometric correction, these values correspond to $10^{10}\text{--}10^{11}$ photons per flash.

Indirect support comes from the in vitro quantum yield measurements of Ando et al. (2008), who reacted 2.98×10^{11} luciferin molecules with excess luciferase and obtained $\sim 10^{11}$ total photons (their Fig. 1a), confirming that the quantum yield of ~ 0.41 holds at the absolute scale.^[6] This validates our biochemical bound: if the lantern contains $\sim 10^{11}$ luciferase molecules and each fires once, the maximum output is $\sim 4 \times 10^{10}$ photons—not 10^{14} .

All four independent estimates—our lux-meter measurements, the biochemical bound, and the two converted datasets—converge on $10^{10}\text{--}10^{11}$ photons per flash. The 1924 Ives and Coblenz value (3×10^{14}) stands alone as an outlier by $10^3\text{--}10^4$.

Table 4: Photon emission estimates from independent sources.

Source	Method	Reported value	Photons/flash
Commonly cited	“1/40 candle”	0.025 cd	3×10^{14}
Coblentz (1912) original [†]	Visual photometry	1/400 candle	3×10^{13}
Harvey & Stevens (1928)*	Surface brightness	45 mL	6×10^{11}
Goh et al. (2022)*	Lux meter	1–14 lux	$10^{10}–10^{11}$
Biochemical bound	Enzyme × yield	—	$10^8–4 \times 10^{10}$
This work	Lux meter	0.2–0.5 lux	$10^{10}–4 \times 10^{11}$

[†]“Predominating values” per original text; range was 1/50–1/400 candle.

*Our conversion of published data to photon flux.

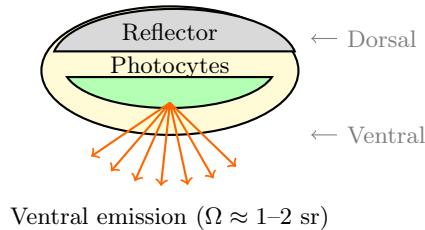


Figure 1: Cross-section of the firefly lantern. The dorsal uric-acid reflector restricts emission to approximately 1–2 steradians; calculations assuming isotropic emission ($4\pi \text{ sr}$) overestimate total photon flux by a factor of 6–12.

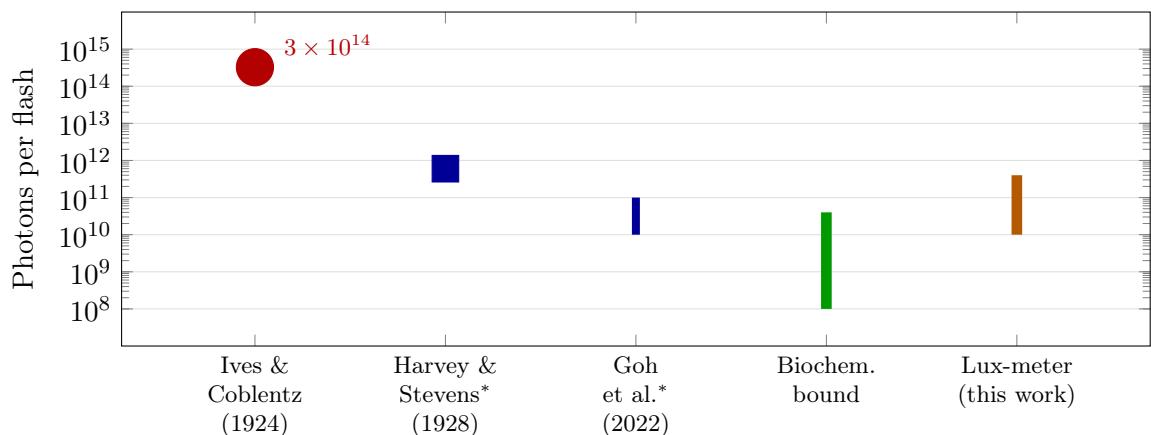


Figure 2: Photon emission estimates from independent sources. The 1924 value (red) is an outlier by 10^3 – 10^4 ; all other estimates converge on 10^{10} – 10^{11} photons per flash. *Our conversion of published data.

117 **4 Discussion**

118 The canonical firefly luminosity value is incorrect by three to four orders of magnitude, and two
119 distinct errors appear to have compounded over the past century.

120 **Error 1: Transcription or rounding.** Coblenz's original 1912 data clearly state that the
121 predominant flash intensity was 1/400 candle, with a maximum of 1/50 candle.^[1] Harvey's treatise^[2]
122 correctly cites this range ("1/50 to 1/400 candle"), yet the value propagated through secondary
123 literature is "1/40 candle"—either a transcription error ($1/400 \rightarrow 1/40$) or a rounded maximum ($1/50$
124 $\approx 1/40$). The erroneous figure appears in educational websites, textbooks, and even a University of
125 Florida compendium that cites "1/50 that of a sperm candle" as the *greatest* recorded intensity for
126 *Photinus pyralis*.^[18]

127 **Error 2: Methodological biases.** Even accepting 1/400 candle as the original measurement,
128 Coblenz's visual nulling photometry introduces several systematic biases when applied to brief,
129 spectrally narrow emissions: (1) observers tend to match peak rather than time-integrated intensity,
130 inflating the estimate by a factor of 2–4; (2) the candlepower unit assumes isotropic emission,
131 whereas firefly lanterns emit directionally into 1–2 steradians, inflating the estimate by a factor
132 of 6–12; (3) firefly emission peaks at 560 nm, precisely at maximum human photopic sensitivity,
133 potentially causing spectral mismatch relative to broadband reference lamps; and (4) calibration
134 against the Hefner lamp standard carried approximately 20% uncertainty. These biases multiply
135 rather than add.

136 **Corroborating historical data.** Harvey & Stevens (1928) measured the surface brightness
137 of *Pyrophorus* click-beetle lanterns at 45 millilamberts over a 1 mm² area.^[16,18] Converting this to
138 photon flux yields $\sim 6 \times 10^{11}$ photons per flash—consistent with our measurements and far below
139 the canonical value. Langley and Very's (1890) earlier measurements of *Pyrophorus noctilucus* gave
140 1/1600 candle, also orders of magnitude below the commonly cited firefly value.^[19,1]

141 **Persistence of the error.** The separation between classical photometry and modern biolu-
142 minescence research allowed this error to persist unchallenged. Lynn Faust, author of *Fireflies,*
143 *Glow-worms, and Lightning Bugs*, notes that fireflies appear far brighter to the naked eye than to
144 cameras because their emission sits at peak human photopic sensitivity of 555 nm (personal com-
145 munication). This perceptual amplification may have contributed to the original overestimate, and
146 the subsequent shift toward arbitrary-unit reporting in biochemical studies meant the discrepancy
147 was never confronted directly.

148 Four independent lines of evidence—our lux-meter measurements, the converted Harvey &
149 Stevens data, the converted Goh & Wang spectrometry, and the theoretical biochemical bound—
150 all converge on 10^{10} – 10^{11} photons per flash. This should replace the erroneous value in future
151 references.

152 **Acknowledgments**

153 Muhammad Naqiudeen Yunus (Sungai Petani, Malaysia) conducted the field lux-meter measure-
154 ments.

155 We reached out to bioluminescence experts. Dr. Timothy R. Fallon, a scholar at Scripps Institu-
156 tion of Oceanography studying firefly photobiology, kindly granted permission to be cited (personal
157 communication, Mar 4, 2025). His working estimate for a *Photinus pyralis* flash was 10^8 – 10^9 pho-
158 tons total per flash—consistent with our biochemical model and significantly below the canonical
159 value. Lynn Faust offered the key insight that fireflies appear far dimmer to camera sensors than
160 to the naked eye.

161 **Data Availability**

162 Raw lux-meter data are available from the corresponding author on request.

163 **References**

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