

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Insecta Mundi

Center for Systematic Entomology, Gainesville,
Florida

6-29-2023

Description of the bioluminescent emission spectrum of *Bicellonycha amoena* Gorham, 1880 (Coleoptera: Lampyridae) in Guatemala

Eduardo A. Arrivillaga-Cano

Maria P. Muñoz-Soler

Diegopáblo Pineda

Edgar R. Rosales

Jack C. Schuster

Follow this and additional works at: <https://digitalcommons.unl.edu/insectamundi>



Part of the [Ecology and Evolutionary Biology Commons](#), and the [Entomology Commons](#)

This Article is brought to you for free and open access by the Center for Systematic Entomology, Gainesville, Florida at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Insecta Mundi by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

A journal of world insect systematics

INSECTA MUNDI

0997

Description of the bioluminescent emission spectrum of
Bicellonycha amoena Gorham, 1880 (Coleoptera: Lampyridae)
in Guatemala

Eduardo A. Arrivillaga-Cano

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala

María P. Muñoz-Soler

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala

Diegopáblo Pineda

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala

Edgar R. Rosales

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala

Jack C. Schuster

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala

Date of issue: June 30, 2023

Arrivillaga-Cano EA, Muñoz-Soler MP, Pineda D, Rosales ER, Schuster JC. 2023. Description of the bioluminescent emission spectrum of *Bicellonycha amoena* Gorham, 1880 (Coleoptera: Lampyridae) in Guatemala. *Insecta Mundi* 0997: 1–9.

Published on June 30, 2023 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
<http://centerforsystematicentomology.org/>

INSECTA MUNDI is a journal primarily devoted to insect systematics, but articles can be published on any non-marine arthropod. Topics considered for publication include systematics, taxonomy, nomenclature, checklists, faunal works, and natural history. *Insecta Mundi* will not consider works in the applied sciences (i.e. medical entomology, pest control research, etc.), and no longer publishes book reviews or editorials. *Insecta Mundi* publishes original research or discoveries in an inexpensive and timely manner, distributing them free via open access on the internet on the date of publication.

Insecta Mundi is referenced or abstracted by several sources, including the Zoological Record and CAB Abstracts. *Insecta Mundi* is published irregularly throughout the year, with completed manuscripts assigned an individual number. Manuscripts must be peer reviewed prior to submission, after which they are reviewed by the editorial board to ensure quality. One author of each submitted manuscript must be a current member of the Center for Systematic Entomology.

Guidelines and requirements for the preparation of manuscripts are available on the *Insecta Mundi* website at <http://centerforsystematicentomology.org/insectamundi/>

Chief Editor: David Plotkin, insectamundi@gmail.com
Assistant Editor: Paul E. Skelley, insectamundi@gmail.com
Layout Editor: Robert G. Forsyth
Editorial Board: Davide Dal Pos, Oliver Keller, M. J. Paulsen
Founding Editors: Ross H. Arnett, Jr., J. H. Frank, Virendra Gupta, John B. Heppner, Lionel A. Stange, Michael C. Thomas, Robert E. Woodruff
Review Editors: Listed on the *Insecta Mundi* webpage

Printed copies (ISSN 0749-6737) annually deposited in libraries

Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA
The Natural History Museum, London, UK
National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
Zoological Institute of Russian Academy of Sciences, Saint-Petersburg, Russia

Electronic copies (online ISSN 1942-1354) in PDF format

Archived digitally by Portico.
Florida Virtual Campus: <http://purl.fcla.edu/fcla/insectamundi>
University of Nebraska-Lincoln, Digital Commons: <http://digitalcommons.unl.edu/insectamundi/>
Goethe-Universität, Frankfurt am Main: <http://nbn-resolving.de/urn/resolver.pl?urn:nbn:de:hebis:30:3-135240>

This is an open access article distributed under the terms of the Creative Commons, Attribution Non-Commercial License, which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.
<https://creativecommons.org/licenses/by-nc/3.0/>

Description of the bioluminescent emission spectrum of *Bicellonycha amoena* Gorham, 1880 (Coleoptera: Lampyridae) in Guatemala

Eduardo A. Arrivillaga-Cano

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala
eduardoarrivillaga@gmail.com

María P. Muñoz-Soler

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala
mapu.15017@gmail.com

Diegopáblo Pineda

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala
diegopab.ps@gmail.com

Edgar R. Rosales

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala
rosalesgalvez@gmail.com

Jack C. Schuster

Universidad del Valle de Guatemala (UVG)
01015, 18 Avenida 11-95, Guatemala, Guatemala
jschuster@uvg.edu.gt

Abstract. *Bicellonycha amoena* (Gorham, 1880) (Coleoptera: Lampyridae) usually flies one meter above ground level over grass, water, or open areas, where males produce a simple single flash every 2–4 seconds, having their most active flashing period from mid to late dusk and early night. In addition, nothing else is known about the behavior of this species. We conducted field observations at the “Mayan Golf Club” in Guatemala Department, and Santiago Sacatepéquez, Sacatepéquez Department, Guatemala; and analyzed *B. amoena* flashes with a spectroscope. Fireflies displayed a lime-green bioluminescence color. The male flashing activity began ~30 minutes after sunset and lasted approximately 70 minutes. For *B. amoena*, the spectral composition of the flash is intermediate between those known from twilight-active fireflies and nocturnal-active fireflies.

Key words. Fireflies, spectroscopy, flash pattern.

Resumen. *Bicellonycha amoena* (Gorham, 1880) (Coleoptera: Lampyridae) por lo general, vuela a un metro del nivel del suelo sobre pasto, agua o áreas abiertas, donde los machos producen un destello simple cada 2–4 segundos, siendo más activos desde que inicia a oscurecer hasta principios de la noche. Además de esto, no se conoce más sobre el comportamiento de esta especie. Realizamos observaciones de campo en el “Mayan Golf Club” en el Departamento de Guatemala, y en Santiago Sacatepéquez, Departamento de Sacatepéquez, Guatemala; y analizamos los destellos de *B. amoena* con un espectroscopio. Las luciérnagas mostraron un color de bioluminiscencia verde limón. La actividad de destello del macho comenzó ~30 minutos después de la puesta del sol, y duró aproximadamente 70 minutos. Para *B. amoena*, la composición espectral de su destello es intermedia entre la conocida para luciérnagas de actividad crepuscular y de actividad nocturna.

Palabras clave. Luciérnagas, espectroscopía, patrón de destello.

ZooBank registration. urn:lsid:zoobank.org:pub:512FB867-8E8F-47E6-AD02-B3B13C97C25D

Introduction

Fireflies (Coleoptera: Lampyridae) can be found in various habitats including forests, savannas, grasslands, and swamps; the majority of lampyrids are nocturnal and begin their flight and flashing behavior in the evening twilight (Zaragoza-Caballero and Pérez-Hernández 2014). All lampyrids produce light at some stage in their life cycle. All known lampyrid larvae are bioluminescent, with the possible exception of a lanternless, and allegedly dark undetermined species recently reported from the Amazonian tepuis (Kok et al. 2019). Bioluminescence is produced in the paired larval light organ usually located on the abdomen (Riley et al. 2021). In contrast, adult lampyrids vary greatly in the presence, location, shape, and use of the light organs (Branham and Wenzel 2003). Some lampyrids do not produce light as adults and communicate mainly with pheromones for sexual reproduction (Lloyd 1997; Branham and Wenzel 2003). Larval bioluminescence's main function has been suggested to serve as a defense mechanism or to attract prey (Zaragoza-Caballero and Pérez-Hernández 2014). It has also been suggested that bioluminescence in adult lampyrids is a carryover from the larval stage that eventually evolved into a sexual signal (McDermott 1964; Sivinski 1981; Branham and Wenzel 2003). By morphological data, it is suggested that bioluminescence evolved early during the process of the evolution of cantharoid beetles, and lampyrids seem to have retained bioluminescence from one of these early ancestors (Branham and Wenzel 2001, 2003).

Bioluminescence can be defined as light emission through a chemical reaction produced by living organisms, such as fireflies, certain dipteran larvae, bacteria, fungi, dinoflagellates, and other beetles (such as Elateridae and Phengodidae). The biochemistry of this process consists of the luciferin-luciferase reaction, where a luminescent substance (luciferin) is oxidized by the catalytic action of an enzyme (luciferase). The indispensable components of this system are ATP and magnesium (Ugarova and Brovko 1981; Ilyina et al. 1998; Branchini et al. 2010).

Among fireflies, mate attraction signals are composed of chemical signals (pheromones), glows (continuous light signals), and flashes (short intermittent light signals); the last of which being the most observed (Lloyd 1997; Stanger-Hall et al. 2007). Flashing fireflies tend to be more active at dusk, night, or both, where males and females use species-specific light signals precisely timed to communicate with each other in an interactive visual Morse-code manner that encodes information concerning species identity and sex (Stanger-Hall et al. 2007; Lewis and Cratsley 2008). Males usually initiate the signaling, while in flight. Once a female responds by flashing, a reciprocal courtship dialogue occurs, in which both sexes exchange flash signals. Females flash usually in response to males and remain stationary. Courtship continues until males contact females and copulation occurs. Colors of firefly bioluminescence range widely from green (~546 nm) through yellow and orange (~590 nm), even though the luciferin is identical in all known species (Lewis and Cratsley 2008). The color of the emitted light is only caused by the species-specific enzymes involved in light production (Seliger and McElroy 1964).

To be able to communicate through bioluminescence, fireflies use screening and visual pigments that vary among species allowing variation in the sensitivity of the eye, depending on the time when each species is active (Lall and Lloyd 1989; Cronin et al. 2000). Visual pigments are composed of an opsin (responsible for light detection and overall vision), bound to a chromophore (the structure responsible for light absorption), being R-type opsin primarily responsible for arthropod vision (Wald 1968; Porter et al. 2012; Martin et al. 2015). The screening pigments tune firefly sensitivity in both nocturnal and twilight species (Cronin et al. 2000). It seems likely that when bioluminescence first assumed a role in firefly sexual communication, the luciferase enzyme was selected to produce green bioluminescence emissions to coincide with the spectral sensitivity of the species visual system (Lall et al. 1980, 1982; Seliger et al. 1982a,b).

Molecular evidence suggests that the short wavelength (SW) opsin class has been lost from several beetle lineages, including fireflies (Lampyridae) (Martin et al. 2015; Sander and Hall 2015; Sharkey et al. 2017). All beetles may lack this opsin class (which generally confers visual sensitivity to blue wavelengths in insects); however, physiological studies have revealed that some beetles do have blue sensitive photoreceptors (Hasselmann 1962; Lin and Wu 1992; Lin 1993; Döring and Skorupski 2007; Lord et al. 2016). A recent study has shown that SW opsin class was lost prior to the early evolutionary history of beetles, ~300 million years ago, and blue light sensitivity was regained in numerous lineages of beetles independently of the ancestral SW opsin (Sharkey et al. 2017). Presumptive loss of tri- or di-chromatic color vision under low-light or spectrally-attenuated conditions has little

impact on fitness (Jacobs 2013). It is now known, by analysis through genome and transcriptome sequencing, that fireflies possess only one copy of two opsin classes: long-wavelength-sensitive (LWS) and ultraviolet-sensitive (UVS) (Martin et al. 2015; Sander and Hall 2015; Sharkey et al. 2017).

It has been reported that *Bicellynycha amoena* (Gorham 1880) (Fig. 1) usually flies one meter or less above ground level over the grass and open areas, and males produce a simple single flash every 2–4 seconds at 22–25°C (L. Faust, pers. comm.). This species is distributed from México to Panama (Bohórquez 1996). In Guatemala it occurs at sea level on the Pacific and Atlantic coasts; and in Guatemala City, at 1500m alt. Also, you can see it flashing during at least 10 months of the year depending on the site (Schuster 1997). There has been no published research in Guatemala on *Bicellynycha* since Gorham 1880, in the *Biologia Centrali-Americana*, except for

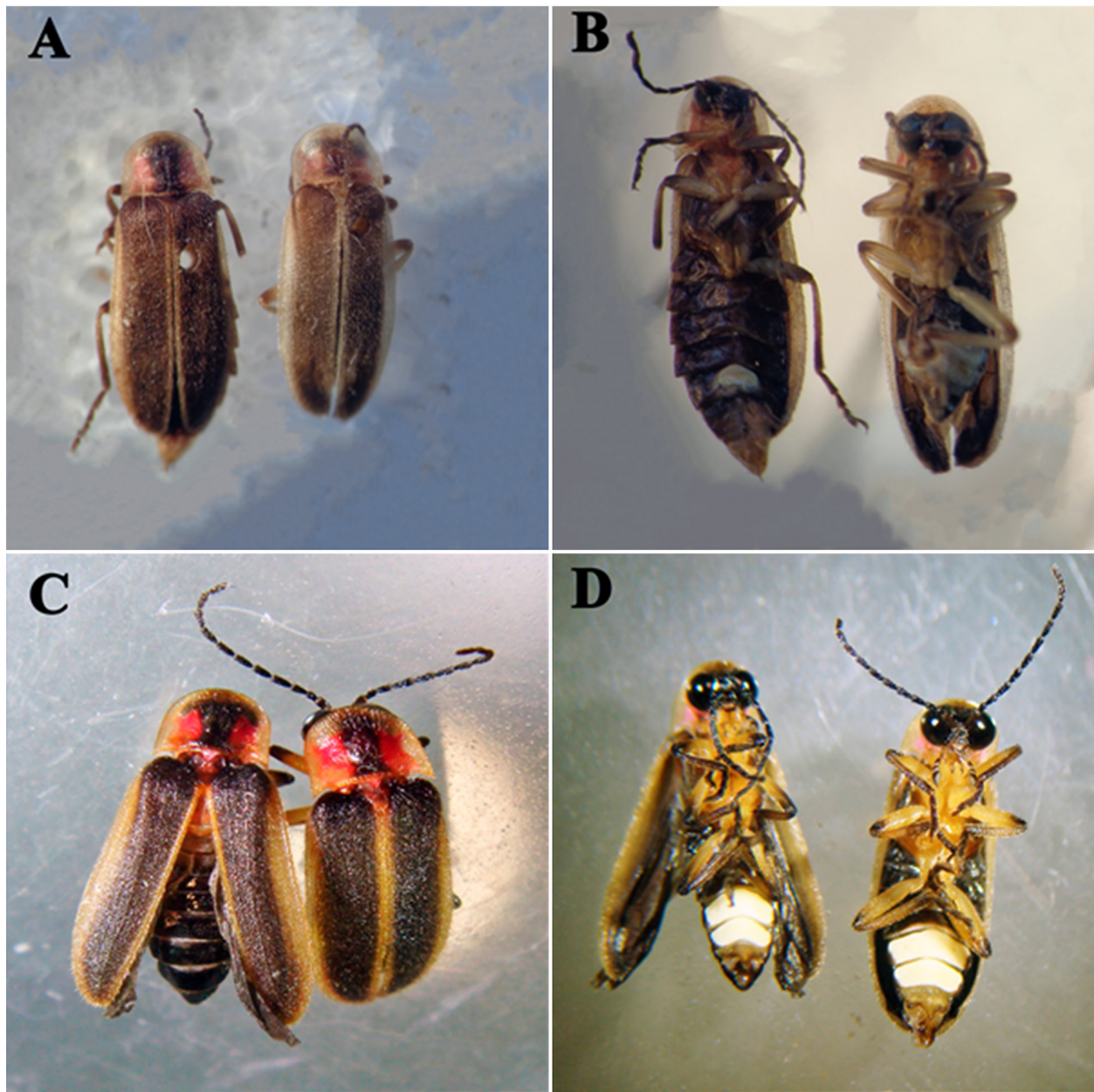


Figure 1. Dorsal and ventral view of *B. amoena*. A–B) Male and female from “Mayan Golf Club”, Villa Nueva, Guatemala. C–D) Two males from Hacienda Sac Chich near Merida, Mexico (credit: Lynn Faust).

Schuster (1997). In general, research on fireflies in Guatemala has been almost non-existent. Firefly behavior and flash patterns can be very important to species identification without collecting them.

Materials and Methods

Field observations of male flash pattern. In October 2015, we observed the courtship behavior of two populations of *B. amoena* (identification done by Dr. Jack Schuster, using an unpublished thesis on a taxonomic review of the genus by Bohórquez (1996)). One population at the “Mayan Golf Club” (MGC) (3 nights) (Fig 1A–B), located at Villa Nueva, Guatemala Department, at 1330 m alt.; and the other one at Santiago Sacatepéquez (SS) (3 nights), Sacatepéquez Department, at 2100 m alt. (Fig. 2). To characterize the flash pattern, we measured the time lapse in seconds between 10 flashes of 5 males, with a chronometer in each site and determined the average time between each flash. A total of 50 flashes were measured in each site, with a slight observed variation. The same person did all this to avoid bias. We also measured the environmental temperature with an iPhone using The Weather Channel app (www.weather.com/). To describe the flashing activity, we express the time as “Minutes after sunset”. Voucher specimens were collected and deposited in La Colección de Artrópodos de la Universidad del Valle de Guatemala (UVGC), Guatemala City.

Spectroscopic measure of bioluminescence. Five males and five females from each site were collected with a butterfly net. In the optic laboratory of the Universidad del Valle de Guatemala (UVG), we determined with a spectroscope (© WINSOCO) and with the help of rapid sequential photos the spectrum composition of bioluminescence of 20 *B. amoena* individuals in total. To do this, we held each firefly and placed its light organ on the lens of the spectroscope and induced their glowing behavior by touching their bodies gently with a feather (this was done in a dark room). We also determined whether there was a significant difference between populations in the bioluminescent spectrum using a Wilcoxon-Mann-Whitney U test.

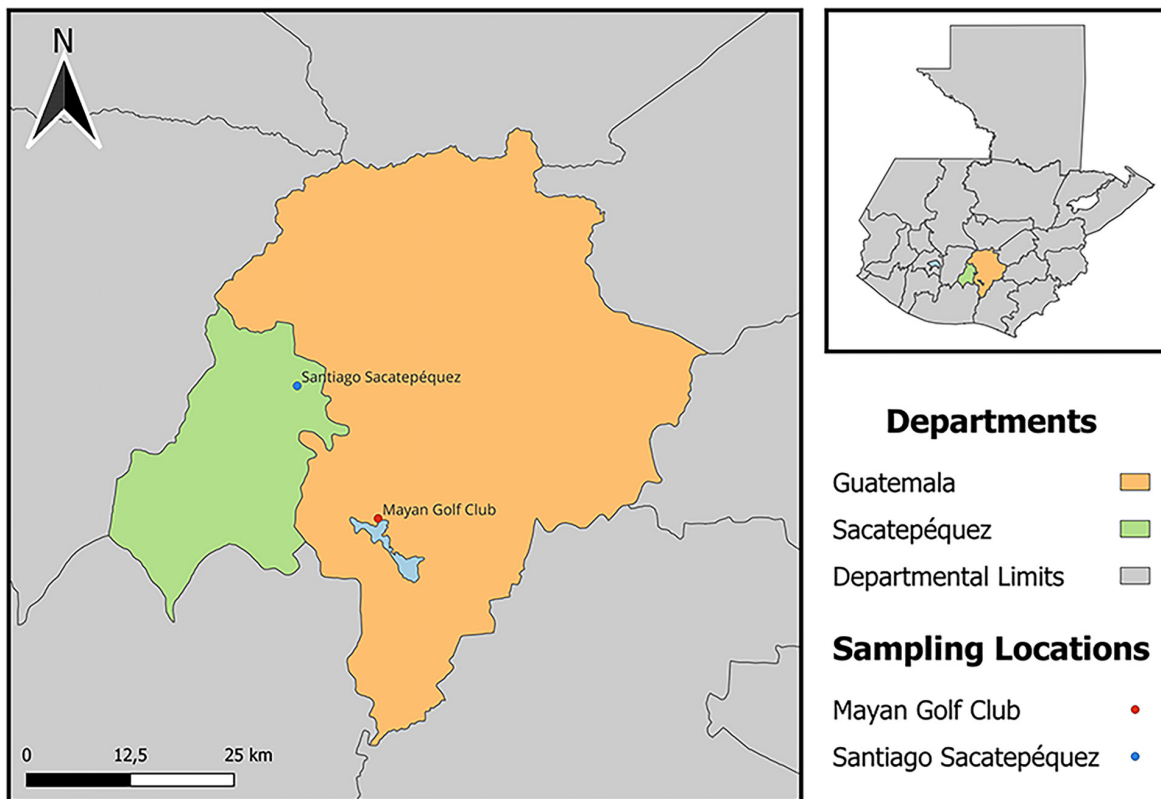


Figure 2. Sampling locations for both populations of *B. amoena* in Guatemala and Sacatepéquez.

Results

Male flash pattern. The time of most flashings of *B. amoena* was from mid to late dusk and early night. The male flashing activity began ~30 minutes after sunset and lasted approximately 70 minutes. We observed that males of the MGC population flew about a meter from the ground surrounding females while females stayed on the grass. In contrast, males of the SS population, similarly to females, remained at the tip of the leaves of the grass. The flash of the males lasts a few milliseconds, while that of the females lasts approximately one second. At 17°C, males in the SS population flashed every 6.21 sec, and at 20°C, at the MGC population, every 6.02 sec.

Bioluminescent emission spectrum. The light from the lantern of *B. amoena* appears yellowish-green. Spectroscopy measurements confirm a lime-green color. On average, the shortest wavelength present in the spectrum of bioluminescence of both males and females at the SS population is 530 nm; and the longest is 626 nm. At MGC population for both sexes, the shortest average is 526 nm, and the largest is 615 nm. There is no significant difference between populations in terms of which wavelength was the shortest and largest within the wavelength range of the bioluminescence spectrum ($z = -1.63$, $p > 0.05$, $n = 10$; $z = -0.92$, $p > 0.05$, $n = 10$ respectively). On average, the shortest wavelength present in the bioluminescence spectrum of *B. amoena* is 528 nm, and the largest is 621 nm. The wavelength of maximum intensity (peak wavelength) is 565 nm (Fig. 3). It is comparable to that of the North American species *Photinus consanguineus* (LeConte, 1852), *Photinus consimilis* (Green, 1956), *Photinus sabulosus* (Green, 1956), and *Photinus umbratus* (LeConte, 1878) (Fig. 4).

Discussion

Although it is known that *B. amoena* flies approximately one meter over the grass (L. Faust, pers. comm.), in the SS population, both males and females remain at the tip of the leaves of the grass until a female responds to a male. After this, the successful male goes to where the female is. This strange behavior probably occurs in this population because of their thermal limit for flight. Fireflies rarely fly below 10°C, and some tropical/semi-tropical species have trouble even flying at 18°C (Faust 2017). However, fireflies have been observed flying and flashing at 11°C in Guatemala (J. Schuster, pers. obs.). Fireflies in this population were active at 17°C or less the nights they were observed. Santiago Sacatepéquez is located at a high elevation (2100m alt.), and in October to January, it has temperatures of 11.8–14.3°C min. and 22.8–23.3°C max. (INSIVUMEH 2022). The finding of

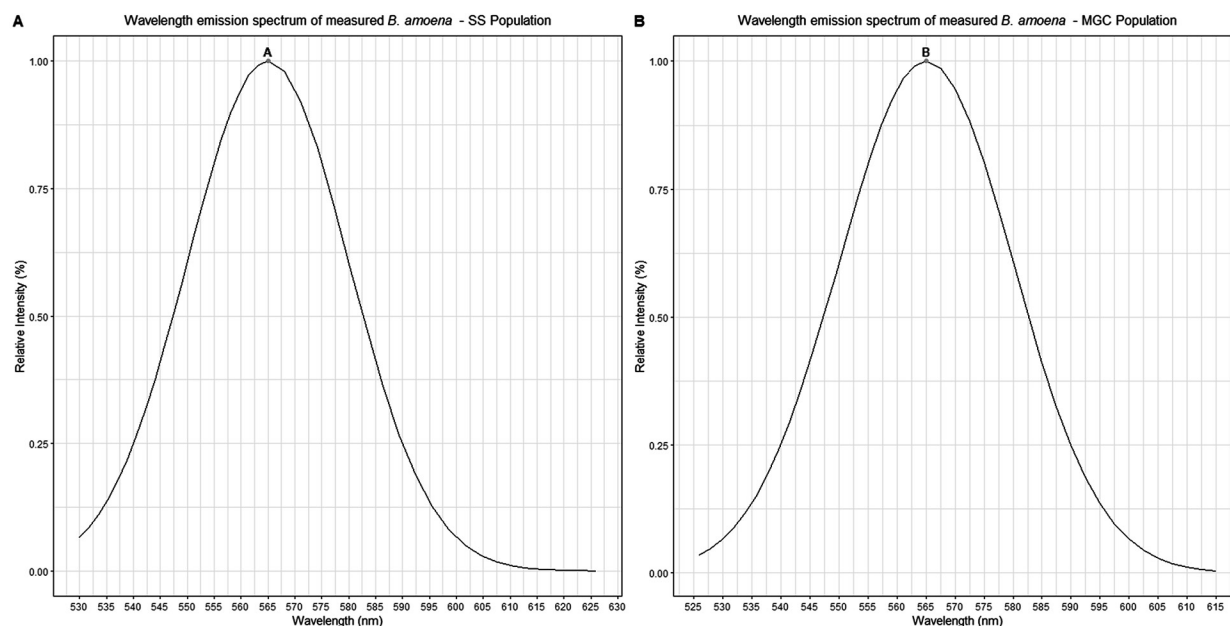


Figure 3. Bioluminescence emission spectrum of *B. amoena*. **A)** SS population. **B)** MGC population.

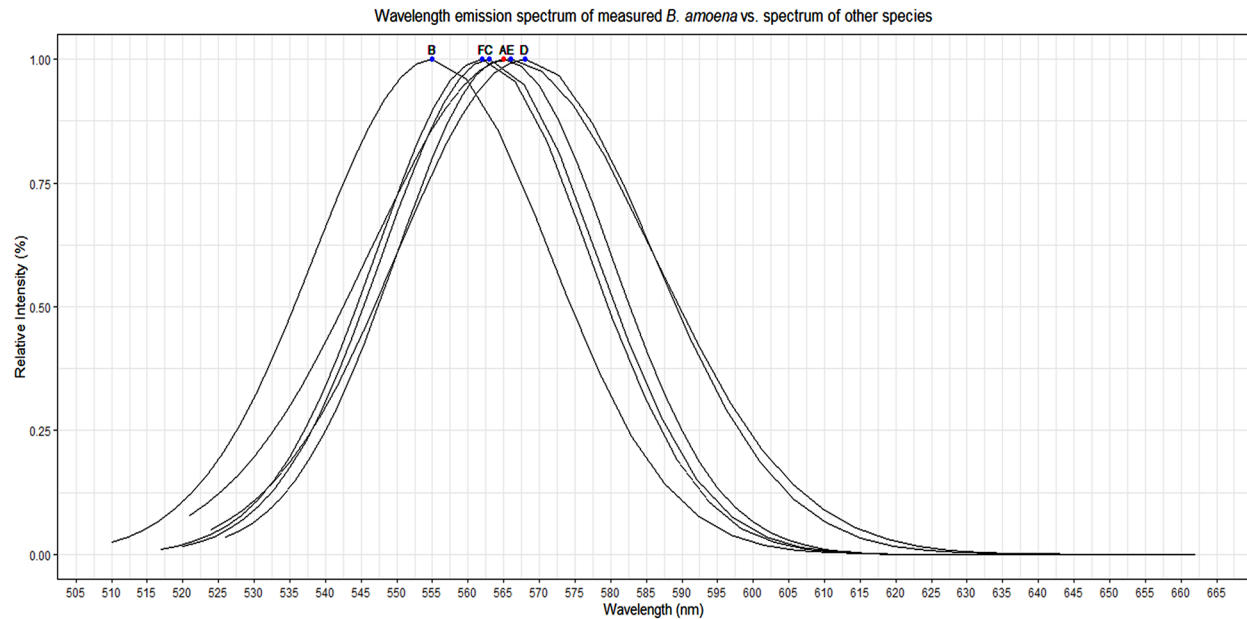


Figure 4. Bioluminescence emission spectrum of *B. amoena* in comparison to that of some North American *Photinus* species. **A)** *B. amoena*. **B)** *P. tanytoxus*. **C)** *P. consanguineus*. **D)** *P. consimilis*. **E)** *P. sabulosus*. **F)** *P. umbratus* (Biggley et al. 1967).

these fireflies in Santiago Sacatepéquez at 2100m alt. represents the highest altitude reported for *B. amoena* in Guatemala (J. Schuster, pers. obs.).

It is known that the bioluminescence spectrum, in general, varies according to activity time. For example, nocturnal fireflies use shorter wavelengths than crepuscular ones (Lall et al. 1980; Booth 2004). Twilight-active species tend to produce lemon-yellow to yellow-orange flashes, in contrast to nocturnal species which more commonly possess lime-green light (Lall et al. 1980; Seliger et al. 1982a,b). *Bicellonycha. amoena* is a two-night species (species that initiates flashing late at twilight and continue into the night) (Lall et al. 1988, 2023); it presents a lime-green bioluminescence color. Assuming that the spectral emission reflects the spectral sensitivity, we infer *B. amoena* has a visual spectral sensitivity intermediate between twilight and nocturnal-active fireflies, with only some attenuation of sensitivity in the green portion of light.

It is possible that this intermediate visual spectral sensitivity allows *B. amoena* a strategy of early emergence to avoid predation pressure from dark-active aggressive mimics of the genus *Photuris* (Lloyd 1975), which have been reported in Guatemala (Gorham 1881, Schuster 1997); and thus balance the reproductive success of the species with the loss of general visual efficiency. While there is no published reference of *Photuris* predation on *Bicellonycha*, there is an observation by Dr. Schuster of *Photuris* sp. 1 eating *Bicellonycha* sp. 1 at Puerta Parada, Santa Catarina Pinula, Guatemala at 1840m alt. during field observations. He also observed that *Bicellonycha* and *Photinus* species from Puerta Parada flash 30 minutes before *Photuris* species, overlapping signaling periods at night. At Puerta Parada, *Bicellonycha* sp. 1, *Photuris* sp. 1 and sp. 2 coincide in April to May; *Bicellonycha* sp. 2 and *Photuris* sp. 1 coincide in June to July; and *Bicellonycha* sp. 2 and *Photuris* sp. 3 coincide in August to September (Schuster 1997), showing overlapping phenologies between genera.

Loss of general visual efficiency occurs when the visual spectral sensitivity is further narrowed and shifted to operate during twilight (Seliger et al. 1982b). This is because, while night-active fireflies utilize a single broad peak sensitivity across the green portion of the visible spectrum, twilight-active fireflies utilize a narrow peak sensitivity in the yellow portion, in addition to a marked attenuation in the green portion by screening pigments (Lall et al. 1980, 1982, 1988; Lall and Worthy 2000). This characteristic gives the twilight-active fireflies an improved detection ability of bioluminescent signals by an increased spectral specificity to filter a significant amount of environment non-informative light, but this also represents a tradeoff with general visual efficiency (Seliger et al. 1982a, 1982b; Lall and Lloyd 1989).

Another possible explanation for intermediate spectral emission and bioluminescence may be that having a higher sensitivity to the green portion of the visible spectrum than the pure twilight-active fireflies allows for a little less specificity in signals detection but a greater ability to detect low-intensity signals and also detect flashes in a green foliage environment in low illumination conditions when contrast with the background is less important (Seliger et al. 1982a; Lall and Lloyd 1989; Booth 2004; Lall et al. 2009). It would be interesting to observe the behavior of this firefly during the totality phase of the next solar eclipse on April 8, 2024; to understand better and elucidate the findings of this research (Branham and Faust 2019).

We registered a simple single flash every 6.21 sec. at 17°C from *B. amoena* males in the SS population, and every 6.02 sec. at 20°C from *B. amoena* males in the MGC population, instead of the pattern of a simple single flash every 2–4 seconds registered at a 22–25°C temperature range by Lynn Faust (pers. comm.). This phenomenon is well known and has been observed for other firefly species. The flash response delay in females and the flash-dark interval from one flash to the next in males are very temperature dependent. Both change inversely with temperature; the hotter the environment, the faster it will be, and the colder, the slower (Lloyd 1966; Faust 2017).

We did not find a significant difference in wavelength between populations. The wavelength range of their bioluminescence spectrum led us to hypothesize that for *B. amoena*, the spectral composition of bioluminescence enhances the ability of the firefly to detect the flash pattern, thus enabling the identification of a potential mate of the suitable species for copulation. The fact before mentioned also supports this; the flash response delay in females and flash-dark interval in males is very temperature dependent (Lloyd 1966; Faust 2017). It is possible that *B. amoena* can distinguish light signals based on the spectrum composition (chromaticity) and discriminate what light signal and pattern belong to a member of his own species, as was demonstrated by Booth (2004) and colleagues with *Lampyrus noctiluca* (L.). It is important to mention that this is an exploratory study, and as such, further work is required to understand and determine the visual spectral sensitivity, spectral tuning, and color vision of *B. amoena* by electroretinogram experimentation.

Conclusions

In the SS population, both males and females remained at the tip of the leaves of the grass until a female responded to a male. This strange behavior may occur in this population because of their thermal limit for flight. Fireflies rarely fly below 10°C, and some tropical/semi-tropical species have trouble even flying at 18°C, so it is not surprising that this population does this because fireflies in this population were at 17°C or less during the nights they were observed.

The presence of the SS population at 2100m represents an extension in the altitudinal range since the highest altitude reported in Guatemala for *B. amoena* was 1500m alt.

In this study, we infer *B. amoena* has a visual spectral sensitivity intermediate between twilight and nocturnal-active fireflies, with only some attenuation of sensitivity in the green portion of light.

Further work is required to understand and determine the visual spectral sensitivity, spectral tuning, and color vision of *B. amoena*. Another question that needs to be resolved for Guatemalan fireflies is: Do species that fly simultaneously have similar spectral characteristics?

Acknowledgments

We thank the engineer Luis Mijangos for his assistance during the spectroscopic measure of the bioluminescence. Special thanks to Lic. José Miguel Morales, Lic. Claudia Quinteros, Lic. Gerardo Estrada and Lic. Jenny Hernández for their assistance and support during the investigation. We also thank Mayan Golf Club and the Rosales Gálvez Family for opening their doors to this research. Finally, we sincerely thank Lynn Faust, Ana Catalán, and Luiz Lima Da Silveira for their support, advice, and help as reviewers. Also, special thanks to Lynn Faust for the photos of *B. amoena* she shared with us, and Abner Lall for his constructive feedback.

Literature Cited

- Biggley WH, Lloyd JE, Seliger HH. 1967.** The spectral distribution of firefly light. II. *The Journal of General Physiology* 50: 1681–1692.
- Bohórquez I. 1996.** Studies toward the taxonomic revision of *Bicellonycha* Motschulsky, 1853 (Coleoptera: Lampyridae: Photurinae). University of Florida; Gainesville, FL. 193 p.
- Booth D. 2004.** Colour vision in the glow-worm *Lampyrus noctiluca* (L.) (Coleoptera: Lampyridae): Evidence for a green-blue chromatic mechanism. *Journal of Experimental Biology* 207: 2373–2378.
- Branham MA, Faust LF. 2019.** Firefly flashing activity during the totality phase of a solar eclipse. *Entomological News* 128: 191–203.
- Branham MA, Wenzel JW. 2001.** The evolution of bioluminescence in Cantharoids (Coleoptera: Elateroidea). *The Florida Entomologist* 84(4): 565–586.
- Branham MA, Wenzel JW. 2003.** The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* 19: 1–22.
- Branchini BR, Ablamsky DM, Rosenberg JC. 2010.** Chemically modified firefly luciferase is an efficient source of near-infrared light. *Bioconjugate Chemistry* 21: 2023–2030.
- Cronin TW, Järvilehto M, Weckström M, Lall AB. 2000.** Tuning of photoreceptor spectral sensitivity in fireflies (Coleoptera: Lampyridae). *Journal of Comparative Physiology A* 186: 1–12.
- Döring TF, Skorupski P. 2007.** Blattfarben von wirts- und nichtwirtpflanzen im wahrnehmungsbereich des kartoffelkäfers (Coleoptera: Chrysomelidae). *Entomologia Generalis* 29: 81–95.
- Faust LF. 2017.** Fireflies, glow-worms, and lightning bugs! Identification and natural history of the fireflies of the eastern and central United States and Canada. University of Georgia Press; Athens, GA. 375 p.
- Gorham HS. 1881.** Insecta. Coleoptera. Malacodermata. Lampyridae. *Biologia Centrali-Americana* 3(2): 29–65.
- Hasselmann EM. 1962.** Über die relative spektrale Empfindlichkeit von Käfer- und Schmetterlingsaugen bei verschiedenen Helligkeiten. *Zoologische Jahrbücher* 69: 573–576.
- Ilyina AD, Cerda FR, Estrada BC, Dukhovich AF, Gaona LGJ, Garza GY, Rodríguez MJ. 1998.** Sistema bioluminiscente luciferina-luciferasa de las luciérnagas. Parte I: Propiedades bioquímicas y catalíticas de la enzima luciferasa. *Journal of the Mexican Chemical Society* 42(3): 99–108.
- INSIVUMEH. 2022.** INSIVUMEH – Instituto Nacional de Sismología, Vulcanología, Meteorología e Hidrología Available at <https://insivumeh.gob.gt/> (Last accessed June 2023.)
- Jacobs GH. 2013.** Losses of functional opsin genes, short-wavelength cone photopigments, and color vision: A significant trend in the evolution of mammalian vision. *Visual Neuroscience* 30: 39–53.
- Kok PJR, van Doorn L, Dezfoulian R. 2019.** Predation by non-bioluminescent firefly larvae on a tepui-summit endemic toad. *Current Biology* 29: R1170–R1171.
- Lall AB, Cronin TW, Bechara EJH, Costa C, Viviani VR. 2009.** Visual ecology of bioluminescent beetles: Visual spectral mechanisms and the colors of optical signaling in Coleoptera, Elateroidea: Lampyridae, Elateridae and Phengodidae. p. 201–228. In: Meyer-Rochow VB (ed.). *Bioluminescence in focus - a collection of illuminating essays*. Research Signpost, Trivandrum; Kerala, India. 385 p.
- Lall AB, Lloyd JE. 1989.** Spectral sensitivity of the compound eyes in two day-active fireflies (Coleoptera: Lampyridae: *Lucidota*). *Journal of Comparative Physiology A* 166(2): 257–260.
- Lall AB, Lord ET, Truth CO. 1982.** Vision in the firefly *Photuris lucicrescens* (Coleoptera: Lampyridae): Spectral sensitivity and selective adaptation in the compound eye. *Journal of Comparative Physiology A* 147: 195–200.
- Lall AB, Seliger HH, Biggley WH, Lloyd JE. 1980.** Ecology of colors of firefly bioluminescence. *Science* 210: 560–562.
- Lall AB, Strother GK, Cronin TW, Seliger HH. 1988.** Modification of spectral sensitivities by screening pigments in the compound eyes of twilight-active fireflies (Coleoptera: Lampyridae). *Journal of Comparative Physiology A* 162: 23–33.
- Lall AB, Viviani VR, Ventura DF. 2023.** Spectral tuning of bioluminescence and visual sensitivity in males of Brazilian firefly species inhabiting dim light environments (Coleoptera: Elateroidea: Lampyridae). *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 339(1): 37–45.
- Lall AB, Worthy KM. 2000.** Action spectra of the female's response in the firefly *Photinus pyralis* (Coleoptera: Lampyridae): Evidence for an achromatic detection of the bioluminescent optical signal. *Journal of Insect Physiology* 46: 965–968.
- Lewis SM, Cratsley CK. 2008.** Flash signal evolution, mate choice, and predation in fireflies. *Annual Review of Entomology* 53: 293–321.
- Lin JT. 1993.** Identification of photoreceptor locations in the compound eye of *Coccinella septempunctata* Linnaeus (Coleoptera, Coccinellidae). *Journal of Insect Physiology* 39: 555–562.
- Lin JT, Wu CY. 1992.** A comparative study on the color vision of four coleopterous insects. *Bulletin of the Institute of Zoology, Academia Sinica* 31: 81–88.

- Lloyd JE. 1966.** Studies on the flash communication system in *Photinus* fireflies. Miscellaneous Publications Museum of Zoology, University of Michigan; Ann Arbor, MI. 96 p.
- Lloyd JE. 1975.** Aggressive mimicry in *Photuris* fireflies: Signal repertoires by femmes fatales. *Science* 187: 452–453.
- Lloyd JE. 1997.** Firefly mating ecology, selection and evolution. p. 184–192. In: Choe JC, Crespi BJ (eds.). *The evolution of mating systems in insects and arachnids*. Cambridge University Press; Cambridge, UK. 387 p.
- Lord NP, Plimpton RL, Sharkey CR, Suvorov A, Lelito JP, Willardson BM, Bybee SM. 2016.** A cure for the blues: Opsin duplication and subfunctionalization for short-wavelength sensitivity in jewel beetles (Coleoptera: Buprestidae). *BMC Evolutionary Biology* 16: 107.
- Martin GJ, Lord NP, Branham MA, Bybee SM. 2015.** Review of the firefly visual system (Coleoptera: Lampyridae) and evolution of the opsin genes underlying color vision. *Organisms Diversity and Evolution* 15: 513–526.
- McDermott FA. 1964.** The taxonomy of the Lampyridae (Coleoptera). *Transactions of the American Entomological Society* 90: 1–72.
- Porter ML, Blasic JR, Bok MJ, Cameron EG, Pringle T, Cronin TW, Robinson PR. 2012.** Shedding new light on opsin evolution. *Proceedings of the Royal Society B: Biological Sciences* 279: 3–14.
- Riley WB, Rosa SP, Lima da Silveira LF. 2021.** A comprehensive review and call for studies on firefly larvae. *PeerJ* 9: e12121.
- Sander SE, Hall DW. 2015.** Variation in opsin genes correlates with signaling ecology in North American fireflies. *Molecular Ecology* 24: 4679–4696.
- Seliger HH, Lall AB, Lloyd JE, Biggley WH. 1982a.** The colors of firefly bioluminescence I. Optimization model. *Photochemistry and Photobiology* 36(6): 673–680.
- Seliger HH, Lall AB, Lloyd JE, Biggley WH. 1982b.** The colors of firefly bioluminescence II. Experimental evidence for the optimization model. *Photochemistry and Photobiology* 36(6): 681–688.
- Seliger HH, McElroy WD. 1964.** The color of firefly bioluminescence: Enzyme configuration and species specificity. *Proceedings of the National Academy of Sciences* 52: 75–81.
- Sivinski J. 1981.** The nature and possible functions of luminescence in Coleoptera larvae. *The Coleopterists Bulletin* 35(2): 167–179.
- Schuster JC. 1997.** Seasonal diversity of fireflies (Coleoptera: Lampyridae) in a montane area of Guatemala. p. 281–284. In: Ulrich H (ed.). *Tropical biodiversity and systematics. Proceedings of the International Symposium on Biodiversity and Systematics in Tropical Ecosystems, Bonn, 2–7 May 1994*. Zoologisches Forschungsinstitut und Museum Alexander Koenig; Bonn, Germany. 357 p.
- Sharkey C, Fujimoto M, Lord N, Shin S, McKenna D, Suvorov A, Martin G, Bybee S. 2017.** Overcoming the loss of blue sensitivity through opsin duplication in the largest animal group, beetles. *Scientific Reports* 7(8): 1–7.
- Stanger-Hall KF, Lloyd JE, Hillis DM. 2007.** Phylogeny of North American fireflies (Coleoptera: Lampyridae): Implications for the evolution of light signals. *Molecular Phylogenetics and Evolution* 45: 33–49.
- Ugarova NN, Brovko LY. 1981.** Bioluminiscencia y análisis bioluminiscente. Universidad Estatal de Moscú; Moscow. 139 p.
- Wald G. 1968.** Molecular basis of visual excitation. *Science* 162: 230–239.
- Zaragoza-Caballero S, Pérez-Hernández CX. 2014.** Biodiversidad de cantaroides (Coleoptera: Elateroidea [Cantharidae, Lampyridae, Lycidae, Phengodidae, Telegeusidae]) en México. *Revista Mexicana de Biodiversidad* 85: 279–289.

Received February 11, 2023; accepted June 7, 2023.

Review editor Oliver Keller.

