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RESEARCH

Artificial Light at Night Reduces Flashing in *Photinus* and *Photuris* Fireflies During Courtship and Predation

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Abstract Artificial light at night (ALAN) affects species-specific communication in a wide range of nocturnal species, including fireflies (Lampyridae). Fireflies rely on bioluminescent signals for communicating. In this study, we conducted two manipulative field experiments to evaluate the effect of artificial light at night on the flashing activity of male and female neotropical fireflies during courtship and predation. Our results showed a significant reduction in the flashing activity of both males and females exposed to ALAN during courtship and predation. Remarkably, the effect of ALAN on male flashing activity seems to be independent of female flashing activity. In conclusion, ALAN disrupts bioluminescent intraspecific (courtship) and interspecific (predation) communication, which in turn could influence mating success, thus negatively affecting neotropical firefly populations in the long term. Our findings contribute to understanding the challenges faced by neotropical firefly communities in the presence of ALAN.

Keywords Anthropogenic effects · communication disruption · intraspecific interaction · interspecific interaction · light pollution

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Introduction

Light pollution is a threat to many nocturnal animal species. Globally, artificial light at night (ALAN) has been gradually increasing in brightness, with an average annual growth of 6%, although it can be as high as 20% in some countries (Hölker et al. 2010). This increment poses a problem for species adapted to respond to changes in light natural cycles (e.g., es daily, lunar, and seasonal) (Navara and Nelson 2007). ALAN disrupts the sensory information used by organisms to interpret and interact with their surroundings (Wakefield et al. 2015) and thus can affect trophic interactions (Maggi et al. 2020) and reproductive activities (Longcore and Rich 2004), which in turn can affect the fitness of individuals (Fobert

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et al. 2019). ALAN is one of the main factors driving the decline of nocturnal animal populations, especially those relying on visual communication such as Lampyridae (fireflies) (Owens and Lewis 2018; Lewis et al. 2020; Fallon and Heckscher 2021). Despite significant advances in our understanding of the ecological consequences of ALAN, its effects on the behavior of neotropical firefly species, is still poorly understood. Furthermore, the lack of information on this topic (but see Owens and Lewis 2018 for a review) is a major problem to be addressed given that fireflies are culturally, ecologically, and economically important. Fireflies are considered bioindicators of ecosystem health (Viviani 2001;Berge 2022) and have become an important nocturnal ecotourist activity (Lewis et al. 2021).

ALAN can affect intra- and interspecific interactions in fireflies because they rely on bioluminescent signals (Owens and Lewis 2018). Bioluminescent cues (e.g., flashes) are specific to nocturnal species and provide information concerning species identity, sex, and mate quality (Lewis et al. 2020). For example, during courtship, the males of the genera *Photinus* and *Photuris* produce species-specific flash patterns while the females wait in the vegetation to respond back (Buschman 2016). During predation, female *Photuris* mimic the courting light patterns of *Photinus* to attract male *Photinus (*Zorn and Carlson 1978; Eisner et al. 1997). This suggests that ALAN can make the flashes harder to perceive and thus interfere with the ability to locate potential mates and prey. Adverse effects on courtship and predation patterns have been shown in previous studies in temperate areas (Costin and Boulton 2016; Firebaugh and Haynes 2016) but how generalizable is this phenomenon in neotropical areas is still not clear. Evaluating the ecological consequences of ALAN may become increasingly urgent in tropical countries where both population growth and increased urbanization are correlated with an increment in light pollution (Bennie et al. 2015).

Fireflies are distributed worldwide but most of its diversity is in the Neotropics and the Asian Southeast (Lawrence and Newton 1995; cited in Vaz et al. 2023), and about halve of the species just in the tropics (Hogue 1993; cited in Stirr 2003). Despite this, neotropical fireflies have been less studied and much of what is known has been extrapolated from other North American species (Hogue 1993; cited in Stirr 2003) including its responses to ALAN. One of the few neotropical studies experimentally investigating the effect of ALAN on fireflies showed that artificial light from lamps negatively impact the occurrence and flashing activity of *Photinus sp.* (Hagen et al. 2015). Although it is an important contribution the study did not consider LED-lamps–a broad spectrum energy-saving technology that is becoming widely popular (Elvidge et al. 2010) and, other behaviors such as mating, and predation which are sensitive to environmental light conditions. Thus, further experimental evidence for effects of ALAN is lacking.

Here we evaluated the effect of ALAN on courtship and predation in neotropical fireflies of the genera *Photinus* and *Photuris*, two of the dominant genera in the neotropics (Hogue 1993; cited in Stirr 2003). Thus, we aim to test if, when exposed to artificial light from commercial white-light LED lamps (Halux) during activity hours, fireflies would reduce their flashing behavior. To investigate this, we designed two independent experiments: courtship and predation, created six replicated mesocosms with controlled firefly density and sex ratios, and measured the number of flashes produced by the fireflies.

Methods

Study Area and Species

A total of 171 Fireflies (*Photinus* and *Photuris*) were captured of which 114 were males and 57 females while they engaged in bioluminescent displays in Tobia, Cundinamarca, Colombia (5,11276, -74,44806), from May 29th to June 4th, 2022. Individuals were captured with butterfly nets and by hand from 20:00 h to 21:30 h. In the field, fireflies were identified using magnifying glasses (40X, 25 mm, Biologika) and field stereoscopes (8-35X, EZ4, Leica) to morphospecies following (Zaragoza-Caballero et al. 2020). Once identified, *Photinus* individuals were stored in aquarium-like terrariums (40 cm x 20 cm x 35 cm) provided with soil, branches, and leaves, and *Photuris* individuals were maintained individually in plastic or glass 200 ml containers to avoid cannibalism. Containers had a damped cotton wad to provide water and were secured with mesh fabric to ensure oxygen (Fig. S1). Individuals were kept at ambient temperature with a natural photoperiod until the start of the experiments. All the experiments were carried out after sunset, at 18:30, and continued until and 21:00, during the peak of activity of fireflies (Dreisig 1975).

Experimental Setup

We set up six mesocosms that consisted of an experimental tent (2.84 m x 2.84 m x 2.70 m) and a box (30 cm x 30 cm x 30 cm) placed in the middle of it (Fig. 1). The tents were spaced 50 m apart, and the LED lamps were oriented downward, ensuring that no light reached adjacent tents (Fig. S2). Both were floorless and made of mesh fabric to allow the penetration of natural light and facilitate behavioral observations. We randomly assigned three tents to natural light (i.e., control) and three to artificial light (i.e., treatment). Treatment tents had a white-light LED lamps (Halux, 900-Lumen, 10 W, Cool Light, IP65) placed in the center of the roof at the highest point of the tent, 2.7 m from the floor (Fig. 1b). We chose white-light LED lamps because they are currently used by humans and fireflies exhibit spectral sensitivity to those wavelengths (480–680 nm) (Owens and Lewis 2021).

Courtship Experiments

To assess the effect of ALAN on courtship behavior, we used two males and one female of *Photuris sp1*. per trial. We performed 41 trials on May 30th and 31st and June 3rd and 4th (about 10 trials per night) and used a total of 82 males and 41 females. After every trial all fireflies were collected and transported to the laboratory to confirm that the individuals in each trial belonged to the same species.

Predation Experiments

To assess the effect of ALAN on predation behavior, we used two *Photinus sp.* males (prey) and one *Photuris sp2* female (predator) per trial. We performed 16 trials on May 30th and 31st and on June 3rd and 4th (4 trials per night) and used a total of 32 males and 16 females. After each experiment all fireflies were collected and freed where they were caught. This is because for the predation experiment identification to genus was sufficient and could be done in the field.

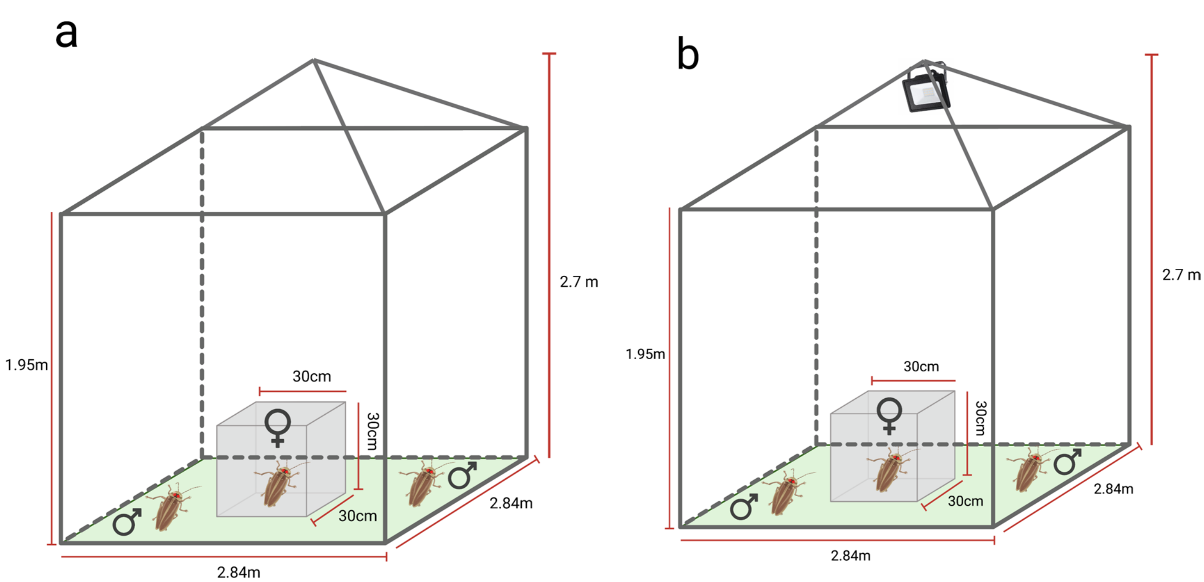

Fig. 1 Scheme of the mesocosm consisting of a tent and a box (indicated by the shadowed cube) situated in the center of the tent. Two types of mesocosms are represented: (**a**) Control mesocosms (natural light) and (**b**) Light treatment mesocosms (artificial light). Artificial light was produced by a 900-lumen commercial LED lamp (Halux, 10 W) placed at the highest point of the tent (2.7 m). In all mesocosms the female was placed on a branch inside the box and males were placed inside the tent and outside the box. Scheme designed with BioRender (https://www.biorender.com)

Data Collection

At the beginning of the trial, we first placed the female inside the box and allowed it to acclimate for ten minutes, after which we introduced the males. Males were allowed to acclimate for three minutes before observations started. In the case of the light treatment, males acclimatized with the light on. After the acclimation period the observers recorded for 15 min the number of flashes emitted by the females, and the males at two distances: near (< 1 m) and far (> 1 m) from the female in the box. Observations were done by one trained observer situated at 1.5 m of distance from the tent. All observers trained in counting firefly flashings on videos until the inter-observer reliability was at least 95% (Landis and Koch 1977).

Characterization of Environmental Conditions

Light intensity and temperature were measured at the start and end of every trial at 30 and 150 cm from the floor using a Vernier LabQuest 2 equipped with light and temperature sensors. In the light treatment we additionally measured the light intensity when lights were turned on. The mean temperature (± SD) in the courtship experiment was 23.3 °C (± 1.295) and for the predation experiment was 23.2 °C (± 0.844) (Table S1). The mean intensity (± SD) of natural light was 1.1 (± 1.47) lux at 30 cm and 1.0 (± 1.9) lux at 150 cm in the control trials and 51.16 (± 47.7) lux at 30 cm and 178.44 (± 164.28) lux at 150 cm in the treatment trials. We had to eliminate 23 measures because the light sensor failed, so to confirm light intensities in the light treatment, we calculated the theorical light intensity using the height, beam angle and lumens of the lamp with the Lamp HQ calculator (https://www.lamphq.com). The theorical values were 237.8 lx at 150 cm and 59.3 lx at 30 cm, which are close to our measurements.

Statistical Analysis

To evaluate the effect of ALAN in the number of flashes emitted during courtship and predation, we fitted a Linear Mixed Model (LMM) with a Gaussian error structure using the package lme4 v.067 (Bates et al. 2015). for each behavior. In both cases, we fitted the total number of flashes produced by males as the response variable, treatment, number of flashes emitted by females (binary: flashed or not), time after sunset (just after sunset, one hour later and two hours later, where sunset occurred at 18:30) as fixed effects, and day of the trial (Julian day) as random effect. We included the time after sunset because the peak of activity varies depending on the species (Lloyd 1980).

To evaluate the effect of ALAN on the female flashing behavior in the courtship and predation experiments, we also fitted an LMM with a Gaussian error structure. We fit the number of flashes emitted by females as the response variable, treatment and time after sunset as fixed effects, and day of the trial (Julian day) as random effect. In all models, the response variable (number of male and female flashes) was centered and scaled to produce coefficients comparable to effect sizes (Rosenthal et al. 1999). All data was processed in R v.4.2.1 (R Core Team 2023) and available in the Online Supplementary Material (Maldonado-Chaparro 2024).

Results

During the study period, we completed a total of 41 courtship trials and 16 predation trials, from which we could not use four courtship trials. Two control trials were excluded because an extra firefly appeared inside the tent, and the other two trials were not finished due to heavy rain. Therefore, our dataset consisted of 37 courtship trials (19 control and 18 light treatment), and 16 predation trials (9 control and 7 light treatment).

Courtship experiments showed a significant difference in the number of flashes emitted by males between control and light treatment (Table 1). Males in light treatment produced a lower number of flashes than control males (Fig. 2a). Furthermore, we found no association between the number of female and male flashes (Table 1; Fig. 2b) suggesting that the effect on male activity is independent from female flashing activity. The same results were obtained when excluding an extreme datapoint and running the analysis (Appendix S1). Firefly activity after sunset showed that male flashing activity decreased two hours after sunset.

Predation experiments showed no difference in the number of flashes emitted by male-prey between control and light treatment (Table 2). Male-preys in the

Table 1 Regression coefficients for the courtship model evaluating the effect of light on the total number of *Photuris sp1* male flashes to female flashes

Predictors	Estimates	SE	DF	t- value	P
Intercept	0.08	0.39	2.82	0.20	0.854
Treatment [light]	-1.01	0.30	26.22	-3.55	**0.002**
Flashes females [1]	0.53	0.34	27.03	1.51	0.143
Time after sunset [2]	-0.17	0.29	31.05	-0.59	0.556
Time after sunset [3]	0.38	0.46	12.69	2.31	0.039
Julian day of experiment	0.29	0.55 (SD)			
Residual	0.41	0.64 (SD)			

Time after sunset had three categories (just after sunset [1], one hour later [2] and two hours later [3]. Bold values denote statistical significance at $P<0.05$. $N=37$ observations (19 control and 18 light treatment). Variance explained by the fixed component ($R^2_M=0.524$) and by the model ($R^2_C=0.723$)

light treatment produced a lower number of flashes than control ones, although this effect was not statistically significant (Table 2; Fig. 2c). We found that male-prey flashed less when female-predator showed no flashing activity (Table 2; Fig. 2d) suggesting a relationship between female and male flashing activity. Firefly activity after sunset showed that male flashing activity decreased two hours after sunset.

Female flashing behavior decrease under light conditions in the courtship and predation experiments, although this result was not statistically significant (Fig. S3). Females emitted a smaller number of flashes compared to control females, in the courtship experiment (Table S2) and in the predation experiment (Table S3). Note that there was no male flashing activity during the light treatment in the courtship (Fig. 2b) and the predation (Fig. 2d) experiments.

Discussion

Our experiment explored the response of firefly flashing activity when exposed to artificial light at night during courtship and predation. Courtship results are consistent with previous studies (Firebaugh and Haynes 2016) and show that males decrease their flashing behavior under light conditions. Nocturnal fireflies have a highly sensitive visual systems that require dark environments to properly work (Lall 1993). This means that ALAN, may affect species-specific patterns of communication by decreasing the bioluminescent activity and/or the efficiency of the signals. Thus, ALAN can disrupt copulation and mating success, consequently the rate of reproduction and survival of fireflies. This scenario is likely to be contributing to the population decline in light-polluted areas.

A reduction in male flashing activity can result from a lack of object recognition, where fireflies are not able to locate or recognize their females (Horridge and Wigglesworth 1969; Bird and Parker 2014). This suggests that ALAN can interfere in the ability to, for example, locate potential mates by lowering and even inhibiting the production of courtship advertisements by male fireflies which can affect the recognition mechanisms involved in mating. In line with previous studies, males decrease their flashing behavior under light conditions (Firebaugh and Haynes 2016); however, contrary to (Firebaugh and Haynes 2016), our response results seem to be driven only by the effect of light as we did not find evidence of an effect of female flashing activity on male flashing activity. This also suggests that ALAN can affect evolutionary processes because it can disrupt the bioluminescent signals that are key for sexual selection (Vencl and Carlson 1998; Lewis and Cratsley 2008), an area that needs to be further explored.

In the predation experiments *Photinus* male flashing activity decreased when exposed to ALAN. Although the difference between control and light conditions was not significant, the observed trend is in line with previous studies (Hagen et al. 2015; Firebaugh and Haynes 2019). The observed decrease in flashing activity may be also driven by changes in *Photuris* females flashing behavior. ALAN may lower the production of mimicked mating-signals

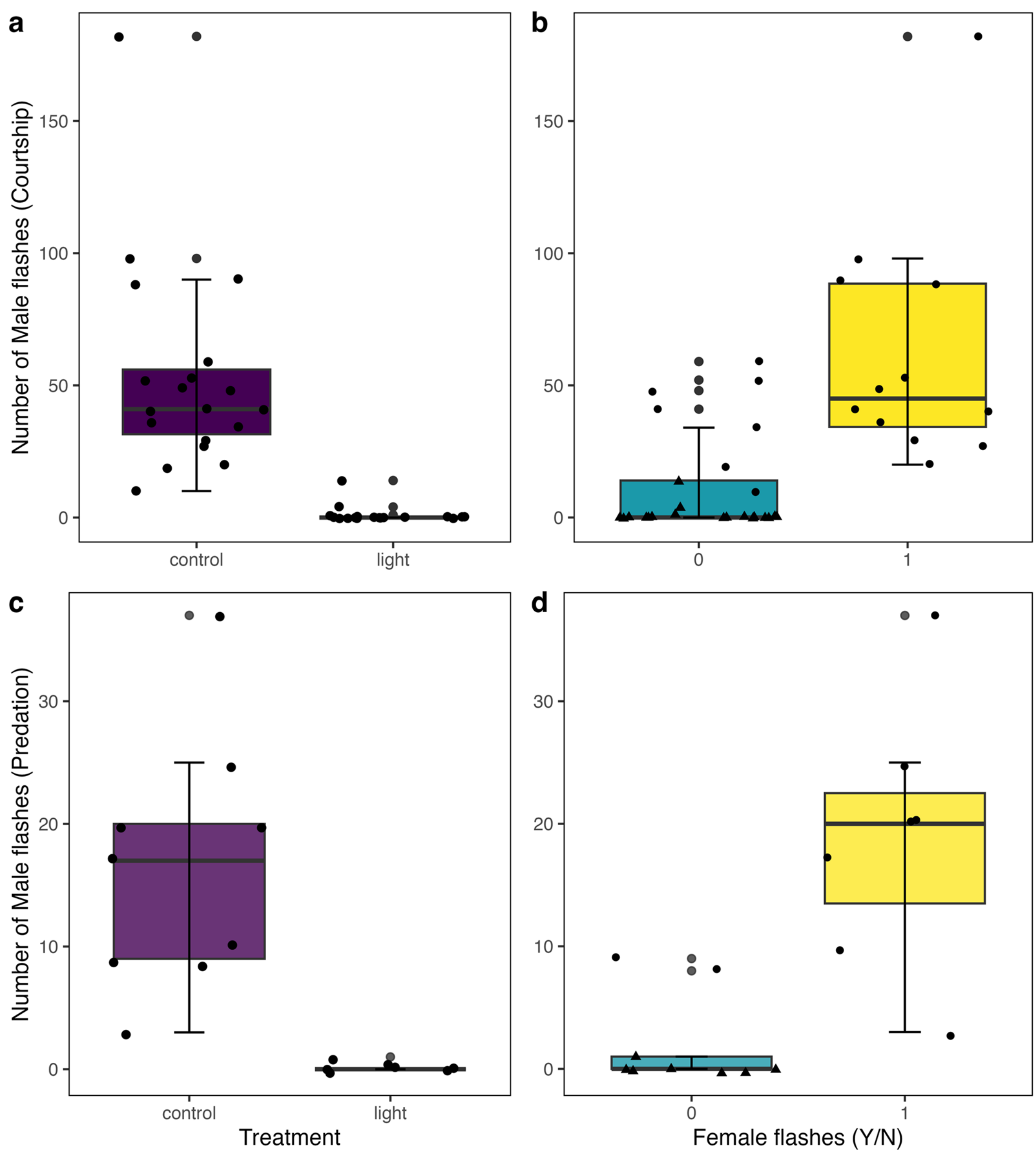

Fig. 2 Responses of the number of male flashes on artificial light treatment (Light, Green box) and natural light (Control, Purple box), and female flashing activity (0 = Blue box, 1 = Yellow box). The upper panel presents the number of flashes of *Photuris sp1* males in the courtship experiment (*N* = 37) in response to the light treatment (**a**) and in relation to the female flashing activity (**b**). The lower panel presents the number of flashes of *Photinus sp.* males in the predation experiment (*N* = 16) in response to the light treatment (**c**) and in relation to female flashing activity (**d**). In panels b and d circles represent control data ($N_{courtship}$ = 19, $N_{predation}$ = 9) and triangles light treatment data ($N_{courtship}$ = 18, $N_{predation}$ = 7). In all panels points were jittered for better visualization. This graph was produced in R version 4.2.1 with the package ggplot2 (Wickham 2016)

thus, disrupting the mimicry behavior in this system. In fireflies of the genus *Photuris*, females imitate the mating-signal of the female prey species (e.g., *Photinus*) to attract male preys (Lloyd 1975). Female predators acquire lucibufagin, a steroid with defensive functions, from the *Photinus* male prey to protect themselves and their eggs (Eisner et al. 1997; González et al. 1999). This raises the possibility that

Table 2 Regression coefficients for the predation experiment evaluating the effect of light on number of *Photinus sp* male flashes to *Photuris sp2* female flashes

Predictors	Estimates	SE	DF	t- Value	P
Intercept	-0.17	0.41	5.33	-0.41	0.698
Treatment [light]	-0.58	0.44	10.89	-1.30	0.221
Flashes females [1]	1.28	0.44	10.89	2.89	**0.015**
Time after sunset [2]	-0.29	0.37	10.11	-0.800	0.442
Time after sunset [3]	-1.77	0.58	10.95	-3.08	**0.011**
Julian day of experiment	0.04	0.19 (SD)			
Residual	0.27	0.52 (SD)			

Time after sunset had three categories (just after sunset [1], one hour later [2] and two hours later [3]. Bold values denote statistical significance at $P<0.05$. $N=16$ observations (9 control and 7 light treatment). Variance explained by the fixed component ($R^2_M=0.729$) and by the model ($R^2_C=0.763$)

ALAN may affect both females and offspring survival, which could negatively impact the dynamics of firefly populations. Nevertheless, additional research is required to confirm this hypothesis and understand the mechanisms at play.

Although our experiments, where light intensity was controlled, showed clear evidence of the effect of ALAN, its effect on firefly flashing communication may vary depending on the differences in light intensity and wavelengths (Owens and Lewis 2018). This indicates that not all types of artificial light may have a negative effect, a hypothesis that requires further exploration to improve our understanding on the effects of ALAN. Thus, a next step would be to evaluate the extent to which different light intensities and wavelengths disrupt firefly behavior. Furthermore, ALAN can also cause spatial and temporal disorientation. First, because light can mask visual information such as that provided by the moon and stars that allow for navigation (Horridge and Wigglesworth 1969; Owens and Lewis 2018) and second, because it alters the typical circadian rhythms of fireflies (Hariyama 2000); however, these topics are still understudied.

We showed that ALAN has a negative effect on courtship and predation behavior in three neotropical species of fireflies of the genus *Photinus* and *Photuris*. However, the mechanisms that are affected by ALAN, such as endogenous diel rhythms, light-sensitive hormone production, or photoreceptor impairment, and the consequences of such effects at the population and community levels, are still unknown. ALAN is the second most important threat to firefly populations around the world (Lewis et al. 2020) hence, studies to further our understanding of the effects of ALAN on different behaviors can be valuable to design proper conservation strategies. This is especially urgent in the tropics, where firefly species are also threatened by habitat loss due to rapid urbanization processes.

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Writing- Review and Editing, Supervision and Project administration.

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Data Availability The raw dataset and scripts to reproduce the analyses are available at:https://osf.io/4hwxd/?view_only=141a207c444947e8abb1082efb48b27d.

Declarations

Ethics All work undertaken in this study was conducted under the permit DVO005 1747-CV1499 granted by the Comité de ética de investigación from the Universidad del Rosario. Fireflies were kept in ventilated enclosures with soaked cotton wads to ensure oxygen and water.

Competing Interests The authors declare no competing interests.

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