

# Costs And Benefits of “Insect Friendly” Artificial Lights Are Taxon Specific

Avalon C.S. Owens (✉ [avalon.owens@tufts.edu](mailto:avalon.owens@tufts.edu))

Tufts University <https://orcid.org/0000-0001-7212-2275>

Caroline Dressler

Brown University

Sara M. Lewis

Tufts University

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## Research Article

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# Abstract

The expansion of human activity into natural habitats often results in the introduction of artificial light at night, which can disrupt local ecosystems. Recent advances in LED technology have enabled spectral tuning of artificial light sources, which could in theory limit their impact on vulnerable taxa. To date, however, experimental comparisons of ecologically friendly candidate colors have mostly considered only one type of behavioral impact, often on only single species. Resulting recommendations cannot be broadly implemented if their consequences for other local taxa are unknown. Working at a popular firefly ecotourism site, we exposed the insect community to artificial illumination of three colors (blue, amber, red) and measured flight-to-light behavior as well as the courtship flash behavior of male *Photinus carolinus* fireflies. Firefly courtship activity was greatest under blue and red lights, while the most flying insects were attracted to blue and amber lights. Thus, while impacts of spectrally tuned artificial light varied across taxa, our results suggest that red light, rather than amber light, is least disruptive to insects overall, and thus more generally insect friendly.

## Introduction

Anthropogenic light pollution, hereafter referred to as artificial light at night or ALAN, is a pervasive perturbation to natural habitats (Falchi et al. 2019; Gaston et al. 2021) that continues to grow in intensity and extent (Kyba et al. 2017; Koen et al. 2018; Li et al. 2020). In recent years, ALAN has become a topic of concern in global change research due to the threat it may pose to the fitness of individuals and functioning of ecosystems (Davies and Smyth 2017; Sanders et al. 2020). In addition to dramatically impacting charismatic fauna such as sea turtles (Weishampel et al. 2016) and bats (Rydell et al. 2020), ALAN has the potential to upset the foundations of global food webs through its increasingly well-documented impacts on plants (Bennie et al. 2018), insects (Owens and Lewis 2018; Owens et al. 2020), and plant-insect interactions (Macgregor et al. 2017; Knop et al. 2017; Giavi et al. 2020).

Numerous recent reports of precipitous declines in the abundance of terrestrial insects (van Klink et al. 2020) and insectivores (Lister and Garcia 2018; Møller 2019) across diverse habitats (Sánchez-Bayo and Wyckhuys 2020) have alarmed researchers, policy-makers, and the public (Saunders et al. 2020; Cardoso et al. 2020). Most experts believe that habitat loss, pesticide use, and climate change are the primary drivers of insect declines (Wagner 2019a; Sánchez-Bayo and Wyckhuys 2019). However, a growing number of commentaries (Grubisic et al. 2018; Wagner 2019b; Owens et al. 2020; Eggleton 2020; Kalinkat et al. 2021) and comparative analyses (van Langevelde et al. 2018; Wilson et al. 2018; Macgregor et al. 2019; van Klink et al. 2020; Wagner et al. 2021) now identify ALAN as a potentially substantial contributor, one which may have been overlooked due to “diurnal bias” on the part of researchers (Rich and Longcore 2006; Gaston 2019). Experimental studies confirm that artificial light can significantly impact the development, movement, foraging, and reproduction of diverse insect taxa (Owens et al. 2020; Kalinkat et al. 2021).

The impacts of ALAN on organisms and populations mainly follow from its interference with the transmission and reception of visual cues. Most animals use natural light cues from the sun, moon, stars, and sky to orient themselves in time and space. If local sources of artificial light obscure the day-night transition, both nightly activities and seasonal development can be delayed (Gaston et al. 2017). If skyglow obscures the moon or stars, animals that use these cues to navigate become disoriented (Dacke et al. 2020; Foster et al. 2021). Navigational disruption sometimes, but not always, culminates in detrimental “flight-to-light” behavior, in which moths, seabirds, and other flying animals circle light sources or perch beneath them, apparently stunned (Verheijen 1960). Finally, artificial light can interfere with detection of the light- or color-based cues of predators, prey, potential mates, or other resources in the environment (Davies et al. 2013; Owens and Lewis 2018; Briolat et al. 2021).

While the long-term impact of ALAN on insect populations remains to be fully quantified (Boyes et al. 2020; Kalinkat et al. 2021), many researchers in the field have nonetheless begun to advocate for immediate conservation action (Owens et al. 2020; Jägerbrand and Bouroussis 2021; Kawahara et al. 2021). Unlike other human disturbances, ALAN is relatively cheap and easy to mitigate, and doing so could quickly alleviate a significant anthropogenic stressor. This realization has inspired trials of various “ecologically friendly” lighting technologies and practices (Azam et al. 2015; Davies et al. 2017; Barroso et al. 2017; Rowse et al. 2018; Fritz et al. 2020; Mészáros et al. 2021) by researchers in search of a win-win conservation strategy that allows the general public to continue using artificial lights for safety and enjoyment without impacting wildlife. One strategy that has attracted much interest is spectral tuning (Longcore et al. 2018): adjustment of the spectral composition of light sources to be minimally disruptive to populations or communities of interest (Zeale et al. 2018; Ayalon et al. 2019; Boom et al. 2020).

Entomological studies generally agree that short wavelengths, particularly UV and blue, are disproportionately attractive to flying insects (Donners et al. 2018; Deichmann et al. 2021), while long wavelengths such as amber and red are less visible to most (but not all) insect species (van der Kooi et al. 2020). However, as described above, flight-to-light behavior is just one of many ways in which ALAN can impact insects and other animals. Despite this fact, few studies to date have assessed the consequences of artificial light for different members of an insect community, which likely vary in their spectral sensitivity and reliance on visual cues (Haynes and Robertson 2021). In particular, little is known about how the wavelengths of light that minimize insect flight-to-light behavior will impact the ability of insects to discriminate visual signals used in mate recognition. These and other possible secondary effects should be investigated before ecologically friendly candidate colors are recommended for broad use.

Fireflies (Coleoptera: Lampyridae) are soft-bodied beetles that employ bioluminescence both as aposematic warning signals and sexual advertisements (Lloyd 1971). Fireflies share several traits with other nocturnal insects, including a discrete activity time defined by ambient light levels (Dreisig 1975, 1980) and a visual system capable of high overall sensitivity at the cost of limited spectral sensitivity (only UV and green photoreceptors; Sander and Hall 2015; Tierney et al. 2017). Their relatively unique ability to bioluminesce, however, sparks intense public interest (Lau and Oakley 2020; Lewis et al. 2020,

2021). Firefly tourism often subjects courtship aggregations to greater levels of artificial light. Previous work has shown that ALAN interferes with the ability of fireflies to both detect (Elgert et al. 2021) and produce (Firebaugh and Haynes 2016) courtship advertisements. In addition, laboratory studies have demonstrated that the degree of interference differs across wavelengths (Owens et al. 2018; Owens and Lewis 2021a). To minimize the impact of ALAN on insect communities writ large, it is essential to determine whether or not the colors of artificial light that minimally disrupt the light-based communication of bioluminescent fireflies are concordant with those that minimize flight-to-light behavior among co-occurring insects.

In this field study, we investigated how spectrally tuned artificial lights influenced two distinct behaviors within the insect community at a synchronous firefly (*Photinus carolinus*) ecotourism site. We experimentally illuminated areas of the site with equally bright red, amber, or blue downwelling artificial light and measured the courtship flash activity of *P. carolinus* males. We simultaneously assessed the attraction of flying insects to the same three light sources using sticky traps. By comparing the relative impact of each color across taxa, we aimed to identify one or more “insect friendly” colors of artificial light that minimally disrupt firefly courtship behavior while also minimizing insect flight-to-light behavior.

## Methods

### Study site and organism

This study was conducted on the grounds of the Kellettsville Firefly Farm, a popular site for synchronous firefly ecotourism located in rural northwestern Pennsylvania (41.5521, -79.2526; 0.16–0.32× above natural night sky brightness levels, from Falchi et al. 2016). The Pennsylvania Firefly Festival (PAFF) has been held annually at this site since 2013; approximately 1000 visitors each year come to view fireflies on a weekend in late June (Lewis et al. 2021). On festival evenings, small groups of visitors are led along the northeast border of the back field and into the surrounding forest, where dedicated firefly viewing areas abut the boundaries of the Allegheny National Forest.

Their synchronous courtship displays make *P. carolinus* Green (1956) the main focus of firefly ecotourism in the United States (Lewis et al. 2021). This species is found in humid forests along the Appalachian mountain range from northern Georgia to western New York (Faust 2010; Walker and Faust 2021). Winged adults are active for a period of around three weeks between May and June, during which time they engage in nightly courtship displays beginning thirty minutes or more after sunset. Dense aggregations of patrolling males emit variable flash trains in loose synchrony: individual flash patterns consist of 4-11 flashes and are followed by 6-9 seconds of darkness, against which inconspicuous females perched below can choose to answer with characteristic doublet response flashes (Faust 2010; Moiseff and Copeland 2020).

### Study design

During peak mating season in summer 2019, we worked along the southwest edge of the back field where dense aggregations of displaying males spilled out from surrounding forest. Four long rectangular plots ( $2.5 \times 10 \text{ m}^2$ ) were established at 30 m intervals along the forest edge; each ran perpendicularly from the forest edge into the field, and was divided into four subplots ( $2.5 \times 2.5 \text{ m}^2$ ) exhibiting a natural gradient in firefly abundance (Figure 1). A shepherd hook pole (height: 2 m above ground) was installed between the two center subplots of each plot, and used to suspend one of four light treatments (Explux PAR38 LED floodlights): blue (peak wavelength  $\pm$  half width at half maximum:  $459.89 \pm 12.15 \text{ nm}$ ), amber ( $610.72 \pm 47.88 \text{ nm}$ ), red ( $633.82 \pm 10.68 \text{ nm}$ ), or an unlit control. Emission spectra were selected in consideration of firefly spectral sensitivity as well as the spectral composition of phosphor-coated white LEDs, which emit both narrow-bandwidth blue and wide-bandwidth amber light; the ratio of these two components determines color temperature. The shepherd hook pole was angled such that illumination from experimental treatments was centered in the middle subplot closer to the field ( $\sim 5.3 \text{ m}$  from the forest edge; Figure 1B).

This light was filtered to a standard intensity ( $1.37 \times 10^{20} \text{ photons cm}^{-2} \text{ s}^{-1}$  measured with an OceanOptics Jaz spectrometer probe at 60.8 cm distance) and shape by means of a variable neutral density filter (Singh-Ray Vari-ND<sup>TM</sup>, diameter: 7.7 cm) suspended at the open end of an otherwise opaque light cage. Each plot was powered by daisy-chained extension cords connected to an outdoor breaker box on the northern end of the field. Two hours before observations began each evening, the light sources were hung in a predetermined random order and each covered with an opaque drawstring bag, after which the three experimental treatments were switched on. This approach allowed each light source time to attenuate to a constant intensity, which took up to 30 minutes in laboratory calibration trials but varied across colors. The drawstring bags were removed immediately prior to the beginning of each trial.

To measure how different colors of artificial light affect *P. carolinus* courtship activity, we counted the number of male flash patterns produced within illuminated and unilluminated plots. Surveys were run between June 16 and July 5, 2019, on clear evenings with temperatures above  $10^\circ\text{C}$  (16 nights total). During each trial, two groups of one or two observers each surveyed all plots twice, first between 22:00 and 23:00 and again between 23:00 and midnight. At each plot, observers surveyed all four subplots twice within a 10-minute period. Each subplot survey lasted 60 seconds: observers recorded the total number of male *P. carolinus* flash patterns that they saw produced within the subplot during that period, and were not asked to interpret whether multiple flash patterns came from the same male or multiple males. When moving within plots between survey periods, observers used dim red headlamps to orient themselves to subplot boundaries, which were demarcated by fluorescent string and wooden dowels wrapped in reflective tape. The order of plot surveys was randomized each night such that both groups of observers were never in the same plot at the same time.

To measure the degree to which flying insects were attracted to the four light treatments, we suspended double-sided sticky traps beneath each light source (15 out of 16 survey nights). The experimental treatments illuminated both sides of the traps equally. Traps were taken down at the end of each trial and installed below their assigned light treatment immediately prior to the next. Traps were replaced at

intervals of one to six days, with briefer intervals later in the season when temperatures were warmer and flying insects were more abundant. Nine nights into the experiment, yellow sticky traps were exchanged for clear window fly traps (Catchmaster traps affixed back-to-back; following Pawson and Bader 2014; Wilson et al. 2021a); data from the yellow sticky traps were ultimately discarded due to concerns that the trap color was more visible under amber light than under blue or red light. Insects caught on each trap during the experiment were identified to order, and flies identified to family, following Castner (2001). Discrete patterns of wing scales on traps were identified as escaped moths. Small numbers of trapped spiders and phoretic mites were omitted from the final analyses.

## Statistical analysis

The impact of light treatment color and subplot position on male flash pattern counts was analyzed in RStudio (version 1.4.1103, R version 4.0.3) using a generalized linear mixed model (GLMM; Bates et al. 2015). Preliminary model competition was carried out using Akaike information criteria to find the data distribution and random effect terms that optimized model fit. The winning model had a Poisson distribution and included light treatment (four levels: dark, blue, amber, and red), subplot position (as a continuous quadratic term), and their interaction as fixed effects; plot, block of time within trial, and day of year were also included as categorical random effects. To compare flash pattern counts under different light treatments within individual subplots, a separate version of this model was constructed with subplot position as a categorical term. In both cases, likelihood ratio tests were used to test the significance of fixed effects (Fox and Weisberg 2019) and multiple comparisons used to understand the impact of individual light treatment colors (adjustments listed in line below; Lenth 2020).

The impact of light treatment color on overall flying insect attraction was analyzed with a negative binomial GLMM, which best accounted for the high variance in insect counts across sticky traps (Brooks et al. 2017). Light treatment was the only fixed effect, and the date of trap removal the only random effect. As both the number of days traps were out and the dimensions of the brands used varied over the course of the experiment, a “trap effort” offset was added to the model, calculated by multiplying the number of days a trap was out by the area (in  $\text{cm}^2$ ) of its sticky surfaces. Differences among light treatments in insect orders and Diptera families caught, hereafter referred to as insect assemblages, were assessed by running permutational multivariate analysis of variance (perMANOVA) on a Bray-Curtis dissimilarity matrix calculated from counts for each taxon, first adjusted for trap effort and then square-root transformed (Oksanen et al. 2020).

## Results

Light treatment significantly impacted the courtship flash activity of male *P. carolinus* fireflies (Poisson GLMM; light treatment: likelihood ratio  $\chi^2 = 94.90$ ,  $df = 3$ ,  $P < 0.0001$ ; Figure 2 **main**). The greatest activity occurred in dark plots ( $0.64 \pm 0.14$  flash patterns per minute, mean  $\pm$  standard error in this and following reports; multiple pairwise comparisons, Tukey adjustment; dark vs. light: Z-ratio  $\geq 7.242$ ,  $P \leq 0.0001$  in all cases), while the lowest activity occurred in plots illuminated by amber light ( $0.03 \pm 0.01$  flash patterns

per minute; Z-ratio  $\leq -3.722$ ,  $P \leq 0.0011$  in all cases). Courtship flash activity was similar under blue and red light ( $0.12 \pm 0.03$  and  $0.17 \pm 0.04$  flash patterns per minute, respectively; blue vs. red: Z-ratio =  $-1.394$ ,  $P = 0.5032$ ).

Light treatment interacted significantly with distance from forest edge (subplot position:  $\chi^2 = 305.11$ ,  $df = 2$ ,  $P < 0.0001$ ; interaction with light treatment:  $\chi^2 = 94.90$ ,  $df = 3$ ,  $P < 0.0001$ ), such that courtship flash activity declined at an approximately linear rate in dark plots as this distance increased, but exhibited a parabolic trajectory under all experimental treatments (Figure 2 **inset**). Light treatment had no detectable impact on courtship flash activity in the subplot at the forest edge (three treatment vs. control comparisons, Dunnett adjustment; Z-ratio  $\leq 2.250$ ,  $P \geq 0.0659$  in all cases), but significantly inhibited courtship flash activity in the two central subplots of all experimental treatments (Z-ratio  $\geq 4.799$ ,  $P < 0.0001$  in all cases); in the subplot farthest from the forest edge, only red light did not significantly impact courtship flash activity (dark vs. blue: Z-ratio =  $2.600$ ,  $P = 0.0260$ ; dark vs. amber: Z-ratio =  $3.146$ ,  $P = 0.0048$ ; dark vs. red: Z-ratio =  $1.216$ ,  $P = 0.4734$ ).

Light treatment also had a significant impact on the number of flying insects caught on nearby sticky traps (negative binomial GLMM; light treatment:  $\chi^2 = 88.29$ ,  $df = 3$ ,  $P < 0.0001$ ; Figure 3), with the fewest insects caught on traps located in dark plots ( $0.05 \pm 0.02$  individuals/cm<sup>2</sup>/day; multiple pairwise comparisons, Tukey adjustment; dark vs. light: t-ratio  $\leq -4.067$ ,  $P \leq 0.0086$  in all cases), an intermediate number attracted to red plots ( $0.19 \pm 0.04$  individuals/cm<sup>2</sup>/day; red vs. amber: t-ratio =  $-6.186$ ,  $P = 0.0003$ ; red vs. blue:  $-5.909$ ,  $P = 0.0005$ ), and equally large numbers attracted to blue and amber plots ( $0.45 \pm 0.09$  and  $0.46 \pm 0.10$  individuals/cm<sup>2</sup>/day, respectively; blue vs. amber: t-ratio =  $-0.340$ ,  $P = 0.9857$ ). Only four fireflies were trapped over the course of the experiment: one under amber light, one under red light, and two under blue light.

Light treatment significantly altered the composition of the insect assemblage captured on sticky traps (perMANOVA of Bray-Curtis dissimilarity matrix;  $F = 4.581$ ,  $df = 3$ ,  $P = 0.0002$ ); test assumptions of multivariate homogeneity of treatment group dispersions were met (permutation test;  $F = 0.431$ ,  $df = 3$ ,  $P = 0.7330$ ). In general, sticky traps placed on unilluminated poles caught proportionally higher numbers of moths and chironomid midges; sticky traps under red or amber light caught higher proportions of psychodid drain flies; and sticky traps under blue light caught higher proportions of tipulid crane flies and caddisflies (Figure 3 **right**). The principal coordinate (PC) analysis dispersion plot (Figure 3 **left**) shows a distinct separation between the insect assemblages caught on sticky traps deployed in dark vs. light plots, and further suggests a continuum of differences among experimental treatments paralleling the visible light spectrum. Insect assemblages caught on sticky traps under red light were closest in composition to those caught on unilluminated sticky traps, while those caught under amber light overlapped with those caught under both blue and red light.

## Discussion

Few studies to date have examined how spectral tuning of artificial lights can impact different behaviors within the same insect community. All three candidate colors that we tested significantly inhibited the synchronous courtship displays of male *P. carolinus* fireflies and also attracted significant numbers of flying insects. As expected, both of these behavioral impacts were more severe under some colors of light than others. Crucially, however, we found that the relative impacts of blue, amber, and red light on firefly courtship flash activity and insect flight-to-light behavior differed, emphasizing the necessity of a cautious approach to “insect friendly” lighting recommendations.

All colors of artificial light significantly reduced firefly courtship flash activity: averaged across subplots and colors, male flash pattern rates in experimental plots were reduced to only 17% of those observed in control plots. As we did not track individuals, this difference could be due to a decline in the number of males present, the flash rate of males present, or both. Previous field studies found that illumination from a white LED floodlight causes nocturnal *Photuris versicolor* fireflies of indeterminate sex to flash at 30% their normal rate (Firebaugh and Haynes 2016), and crepuscular *Photinus pyralis* males enclosed in mesh tents to flash at 75% their normal rate (Firebaugh and Haynes 2019). In laboratory trials, most colors of downwelling artificial light cause semi-nocturnal *Photinus obscurellus* males to flash at around 50% their normal rate (Owens and Lewis 2021a). These data suggest a possible relationship between the temporal niche of a firefly species and its susceptibility to courtship disruption from artificial light. Such a relationship would explain the relatively high sensitivity exhibited by the *P. carolinus* males in this study, which become active at the end of astronomical twilight, later than any other *Photinus* species assessed to date. Future studies might seek to quantify this relationship and investigate whether it extends to other taxa with discrete activity windows.

Distance to an artificial light had a greater impact on firefly courtship flash activity than the color thereof. Across all three experimental treatments, male flash rates were suppressed most strongly within the two central subplots containing or adjacent to the light source. In subplots closest to the forest edge flash rates did not differ among experimental treatments, while in subplots farthest from the forest edge flash rates were significantly suppressed by blue and amber lights only. The difference between subplots on either end may have been due to the offset placement of the light sources (Figure 1B), or to the presence of shade trees along the forest edge, or both. Previous research indicates that both firefly larvae (Owens and Lewis 2021b) and flightless female glow-worms (Elgert et al. 2020) seek cover when exposed to artificial illumination, but the phototaxes of adult flashing fireflies remain mysterious (see Firebaugh and Haynes 2016). Previous studies of other firefly species have shown that ALAN is most disruptive at close range (Hagen et al. 2015; Van den Broeck et al. 2021), its impact abating at distances between 2.3 m (Elgert et al. 2020) and 40 m (Stewart et al. 2020). Similar studies of flight-to-light behavior in moths have found radii of attraction as small as 3 m (Baker and Sadovy 1978; Truxa and Fiedler 2012) and large as 30 m or more (Beck and Linsenmair 2006; Degen et al. 2016). As our fixtures were dim, near to the ground, and fully shielded, the approximately 2.5 m radius of firefly courtship flash suppression we observed should be treated as a conservative estimate.



The impact of artificial light on firefly courtship flash activity also varied by color, but to a lesser degree. Blue and red light caused the smallest reduction in *P. carolinus* male flash activity, and amber the largest (blue and red: 23% the normal rate; amber: 4%). The impact of slightly higher intensities of artificial light ( $2.08 \times 10^{20}$  photons  $\text{cm}^{-2} \text{s}^{-1}$  vs.  $1.37 \times 10^{20}$  photons  $\text{cm}^{-2} \text{s}^{-1}$  here) on *P. obscurellus* male courtship flash activity has also been shown to be spectrum dependent (amber: 32%; blue and red: 47%; Owens and Lewis 2021a). While the ordinal impacts of these colors are similar across these two studies, amber light had a disproportionately strong effect on the *P. carolinus* males in this study. This difference could be due to differences in the spectral sensitivity of these two congeners or, more likely, differences in the spectral composition of the light sources. The amber light employed in this study was relatively broad-spectrum (**Figure S1**), increasing its likelihood of absorption by the long-wavelength photoreceptors that in fireflies are attuned to conspecific bioluminescence (Cronin et al. 2000). It is possible that *P. carolinus* males in amber plots may then have flashed less often because they perceived that their flashes were less visible to females (Johnsen et al. 2004).

All colors of artificial light attracted significant numbers of flying insects. Sticky traps placed under red light captured fewer insects than those placed under amber or blue light, but more than those in dark control plots, likely due to the lack of red photoreceptors in most insects reducing but not eliminating the visibility of long wavelengths (van der Kooi et al. 2020). Surprisingly, although Donners et al. (2018)'s model of insect flight-to-light behavior predicts that our blue light would be by far the most attractive (capturing  $2.71 \times$  as many insects as our red light, vs.  $1.90 \times$  red for amber), it was actually slightly less attractive than our amber light ( $2.32 \times$  red vs.  $2.43 \times$  red, respectively). This difference likely reflects the particular composition of the insect community at our site: Diptera comprised over 85% of our total trap catches but only 43% of the data used to fit Donners et al. (2018)'s model, and many flies are disproportionately attracted to the yellow and/or infrared wavelengths (Wakefield et al. 2016; Wilson et al. 2021b) produced by our broad-spectrum amber light (Figure 1). Insects belonging to other orders were more attracted to our blue light than to our amber light, again demonstrating that spectral tuning in the amber range can benefit some taxa while harming others.

Broad-spectrum amber and warm white light are popular “ecologically friendly” lighting alternatives because both produce relatively low amounts of disruptive blue wavelengths (IDA 2010; Longcore et al. 2018) yet possess sufficient spectral range to allow humans to discriminate colors in their environment (Fotios et al. 2015; Boyce 2019), unlike narrow-spectrum red light. In some contexts, however, nocturnal color discrimination may not be worth attendant ecological costs. Recent studies show that amber has a greater impact on the movement of bats (Straka et al. 2019) and sea turtles (Robinson et al. 2016) than does equally bright red light. Deichmann et al. (2021) have found that, compared to standard warm white LEDs, those that have their blue wavelengths filtered out are less attractive to most insects but more attractive to bioluminescent click beetles and fungus gnats. The disproportionate impacts of amber light on firefly courtship flash activity and flying insect attraction that we observed in this study offer more evidence in support of the use of red lights, when necessary, around natural ecosystems.

Compared to our dark control, red light still significantly inhibited firefly courtship flash activity and attracted significant numbers of flying insects. Furthermore, red light has previously been shown to disorient toads (Buchanan 1993), birds (Goller et al. 2018), and bats (Voigt et al. 2018; Zeale et al. 2018; Straka et al. 2019). Even bespoke “turtle friendly” red LEDs disorient hatchlings at close distance (Robertson et al. 2016). Thus, although red light was least disruptive of the three candidate colors we tested, we urge conservationists to remember that spectral tuning should be the final step of efforts to limit ALAN. Reducing the intensity of a light source, either by dimming it or moving it farther away (as was simulated in edge subplots for this study), has repeatedly been shown to be more effective at minimizing its impact on natural ecosystems (Davies et al. 2017; Owens and Lewis 2021a; Van den Broeck et al. 2021).

Ecotourists are drawn to the Pennsylvania Firefly Festival each summer for the explicit purpose of encountering insects at night. They and other firefly enthusiasts are likely to be more willing than most to adopt insect friendly lighting practices in their own communities, which could simultaneously aid both insect and dark sky conservation efforts (Owens et al. 2020). Until now, however, investigations into the lighting practices that least disrupt firefly courtship and those that least attract flying insects have been carried out entirely separately, with no data to indicate whether putatively “firefly friendly” lighting negatively impacts other insect taxa in the same community, or vice-versa.

ALAN is a novel environmental disturbance that affects animals in complex and variable ways, but one which can be tuned to limit, if not eliminate, its impact on most vulnerable taxa. Future trials of ecologically friendly lighting candidates should include a range of colors, intensities, spatial and temporal distributions, *etc.*, of artificial light, and observe their impact on multiple aspects of the fitness of diverse taxa. Such research may reveal an approach that allows for relatively unrestricted illumination of nocturnal habitats, but such an outcome seems unlikely. For now, the only effective way of reducing the ecological impact of light pollution is, as is the case for any harmful pollutant, to limit its spread.

## **Declarations**

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### ***Conflicts of interest***

The authors declare that they have no conflicts of interest.

### ***Ethics approval***

All applicable institutional and national guidelines for the care and use of insects were followed.

### ***Consent to participate***

N/A

### ***Consent for publication***

N/A

### ***Availability of data and code***

Data and code from this study are available from the corresponding author on reasonable request.

### ***Author contributions***

ACSO, CD, and SML conceived and designed the experiments; ACSO and CD performed the experiments; ACSO analyzed the data and drafted the manuscript; all authors provided editorial advice.

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## Figures

### Figure 1

Map and layout (not to scale) of the summer 2019 field experiment, showing four rectangular plots established at 30 m intervals along the southwestern forest edge. Light treatments (filled circles) were suspended 2 m above the ground from shepherd hook poles installed in the center of each plot. Light treatments were randomly shuffled among plots each evening. **(inset A)** Intensity and spectral distribution of the ExPlux PAR38 blue, amber, and red LED floodlights used in this study, which were filtered to yield identical total photon flux densities. **(inset B)** Magnified top-down view of an individual plot, with four square subplots spanning a natural gradient in firefly abundance. In experimental plots, the cone of light (dashed blue circle) was offset 0.3 m into the center subplot farther from the forest edge. House icon indicates the location of the Kellettville Firefly Farm and footsteps show the route to synchronous firefly viewing areas taken by PAFF attendees.

### Figure 2

Box plots summarizing the number of male *Photinus carolinus* flash patterns observed per minute in dark control plots (grey) and in treatment plots illuminated by one of three colors of artificial light (blue, amber, or red). Male flash activity at each plot was censused independently in each of four subplots at varying distances from the forest edge. LED floodlights were suspended approximately 5.3 m from the forest edge. Asterisks denote significant differences from mean dark control values at  $P < 0.05$  (\*),  $P < 0.005$  (\*\*), and  $P < 0.0005$  (\*\*\*) levels. **(inset)** Quadratic trend in average male flash patterns per minute across subplots, as modelled by a Poisson GLMM, in darkness ( $e^{-0.27+0.32x-0.16x^2}$ ) and under blue ( $e^{1.49-2.17x+0.30x^2}$ ), amber ( $e^{3.82-5.10x+0.86x^2}$ ), and red ( $e^{1.97-2.32x+0.33x^2}$ ) artificial light.

### Figure 3

Diversity and abundance of flying insects captured on sticky traps set in control plots (black) and plots illuminated by one of three colors of artificial light (blue, amber, or red). **(left)** Principal coordinate (PC) analysis beta-dispersion plot visually representing the results of a supervised analysis (*sensu* (Scott and Crone 2021)). PC1 and PC2 were selected to best differentiate insect assemblages among the four light treatments. Unfilled points represent insect diversity data from individual sticky traps; proximity indicates more similar insect assemblages. Filled points represent centroids for each group, and ellipses one standard deviation from the centroid. **(right)** Stacked barplot showing the total number of flying insects captured under each light treatment, with colors corresponding to insect order and Diptera subfamily (Chironomidae to Drosophilidae) when appropriate.

## Supplementary Files

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