Night-lights: Light pollution impacts on fireflies and arthropod communities

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Abstract

Light pollution—artificial nighttime illuminance from luminaries such as streetlights—has dramatically brightened the nighttime landscape (Gaston *et al.* 2014), envelops an increasingly large portion of the globe, and is continuing to spread (Falchi *et al.* 2016a, Kyba *et al.* 2017). Given the biological importance of light as a resource, information source (Gaston *et al.* 2013), and circadian organizer of activities (Kantermann 2013, Fonken and Nelson 2014), the consequences of light pollution for living organisms are expected to be wide-ranging and complex (Gaston *et al.* 2014). In this dissertation, I examined light pollution impacts on arthropods, with a particular spotlight on fireflies. Fireflies are interesting model organisms for this work because many firefly species produce bioluminescent flashes that they use to communicate with potential mates during courtship prior to mating. In chapters 1 and 2, I explore light pollution effects on firefly flash courtship behaviors, movement, and local abundances. My results show that light pollution decreased firefly flash conversations and mating, attracted fireflies, and reduced local abundances of one species. Taken together, these findings suggest light pollution may create demographic traps, luring fireflies into places where they may be less likely to mate. In Chapter 3, I investigate whether firefly abundances and species richness are associated light pollution and urban land cover across large areas. I accomplished this by surveying fireflies across Virginia, and by comparing my survey data with data emerging from Firefly Watch, a national citizen science firefly monitoring program. In addition to finding similar trends in data collected by a professional scientist and by citizen scientists, I showed local light pollution (i.e., within residential properties) to be negatively associated with firefly abundance and species richness. Finally, in Chapter 4, I examined light pollution impacts on arthropod abundances and trophic structure in a two-year manipulative field experiment. My results show a slight increase in arthropod abundances in illuminated versus unilluminated plots in the first year of sampling, but no impact on abundances in the second year of sampling, and no impact on trophic structure. Overall, my work suggests light pollution effects on arthropods may be complex, affecting multiple aspects of a species' behavior, demography, and ecology, and points to the advantages of taking a multi-faceted approach linking small-scale manipulative field studies with larger-scale surveys to illuminate impacts of light pollution on arthropods.

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Introduction

Changing sensory environments present a new challenge for organisms. Because sensory information—light, sounds, and smells—helps organisms interpret and interact with their environments, inputs of new sensory information associated with urbanization—for example, light pollution, noise pollution, and chemical pollution—potentially touch many aspects of organisms' lives (Halfwerk and Slabbekoorn 2015). Studying the consequences of sensory pollution for organisms will become increasingly important as much of the globe rapidly urbanizes (United Nations, Department of Economic and Social Affairs 2014).

One of the most rapid, yet underappreciated, changes associated with urbanization is light pollution (Figure 1). To date, most biological studies of light pollution are lab-based, and concern a narrow swath of global biodiversity (Figure 2). Field-based studies are needed to explore how organisms are responding to light pollution in the wild. These studies are particularly needed for arthropods, a diverse group whose members are abundant in urbanizing landscapes (McIntyre 2000) and represent key players in terrestrial food webs (Yang and Gratton 2014). In this dissertation, I present field-based, manipulative and observational surveys examining light pollution impacts on arthropods. Fireflies are the particular focus of much of this work, as their nocturnal lifestyle and flash-based communication system make them potentially vulnerable to dramatic brightening of the night-time environment from light pollution.

Study system

Fireflies are beetles in the family Lampyridae. There are 120 described firefly species in North America (Lloyd 2004). The adults of many firefly species produce bioluminescent flashes. These flashes allow males and females to identify and communicate with conspecific mates during courtship prior to mating. Males produce species-specific patterns of flashes, and females signal their acceptance of male mates by flashing back (Lloyd 1971).

Due to the unique, flash-based communication system used in courtship, fireflies are ideal for studying effects of light pollution on behavior and mating. Firefly flashing activities are sensitive to environmental light conditions. Flashing begins at or sometime after sunset when ambient light levels are low (Lall *et al.* 1980), and the timing of nightly flashing activities can be advanced or delayed by natural variation in light levels due to cloud cover or the phase of the moon (Allard 1931, Dreisig 1975). The importance of light as a cue for firefly flashing has been corroborated by laboratory behavioral studies, which show that exposure to artificial light can stop or delay the timing of firefly flashing (Rau 1932, Buck 1937, Dreisig 1975, Merritt *et al.* 2012).

Throughout this dissertation, I pay particular attention to two taxonomic groups of fireflies common to the eastern United States (Faust 2017). The first, *Photinus pyralis,* is a widely-distributed species that begins flashing around sunset. The second, fireflies in the genus *Photuris,* begin flashing sometime after sunset, and are predators of fireflies in the genus *Photinus*.

Chapter summaries

In chapter 1, I examined light pollution impacts on firefly abundances, movement, and *Photinus pyralis* courtship behaviors and mating. I found that light pollution has no effect on abundances of the twilight-active firefly species *Photinus pyralis*, but reduced abundances of the dark-active firefly *Photuris versicolor. Photuris versicolor* fireflies were three times more abundant in unlit plots compared to lit plots. In a study of light pollution effects on *P. pyralis* courtship behavior and mating, I found that light pollution disrupts *P. pyralis* flash courtship dialogues. Females were 3 times more likely to flash in unlit plots compared to lit plots. I also explored light pollution effects on firefly movement (i.e., attraction to lights/repulsion away from lights) using a mark-release-recapture method. Because this mark-release-recapture experiment was less insightful than anticipated due to low overall recapture, I re-visited the question of light pollution affects on firefly movement in chapter 2 using a sheet trap method.

In chapter 2, I extended my examination of light pollution impacts on firefly courtship behavior to include a firefly species that begins flashing several hours after sunset, *P. versicolor*. I found that light pollution stops *P. versicolor* courtship dialogues. Neither males not females flashed near artificial lights. I also conducted an experiment intended to examine light pollution impacts on *Photinus-Photuris* predator-prey dynamics, including interactive effects of light pollution and predator presence on *P. pyralis* courtship behavior and mating (i.e., sub-lethal effects). This experiment provided additional evidence that light pollution reduces *P. pyralis* mating. Almost twice as many *P. pyralis* females mated in unlit cages compared to cages lit with

LED lights. However, I found no evidence light pollution affects predator-prey interactions. No firefly prey were eaten in either the lit or unlit treatments.

Evidence that light pollution interrupts firefly courtship dialogues prior to mating and that artificial lights attract fireflies leads to the hypothesis that light pollution may create demographic traps, luring fireflies into areas where they may be less likely to mate and creating areas where rates of immigration and death exceed rates of emigration and birth. In chapter 3, I examined whether patterns of lower firefly abundances (and species richness) in light-polluted areas expected based on this conjecture emerged across a broad geographic area. I surveyed firefly abundances and species richness within residential properties across Virginia and evaluated whether abundances and species richness were associated with light pollution and urban land cover at multiple spatial scales (at the site, within 0-2 km of the site, and within 8-20 km of the site). I also compared results from the data I collected with those emerging from an analysis of data from Firefly Watch, a national citizen science project. Generally, I found similar trends in the data I collected and the data collected by citizen scientists. For example, light pollution at the site was negatively associated with firefly abundance in both datasets. Congruous results emerging from data collected by a professional scientist and by citizen scientists indicates citizen scientists may be able to provide valuable data for monitoring impacts of anthropogenic changes in the environment across large areas.

Finally, in chapter 4, I examined light pollution effects on arthropod abundance and trophic structure. This study was conducted over two years in experimental plots in a grassland system. Here, I found increased arthropod abundances in plots lit by LED lights compared to unlit plots in the first year of sampling, but no effect of light pollution in the second year of sampling. Additionally, I found no evidence for light pollution impacts on arthropod trophic structure. This work suggests that light pollution impacts on communities may change over time, and that both short-term and longer-term studies are needed to fully explore its effects.

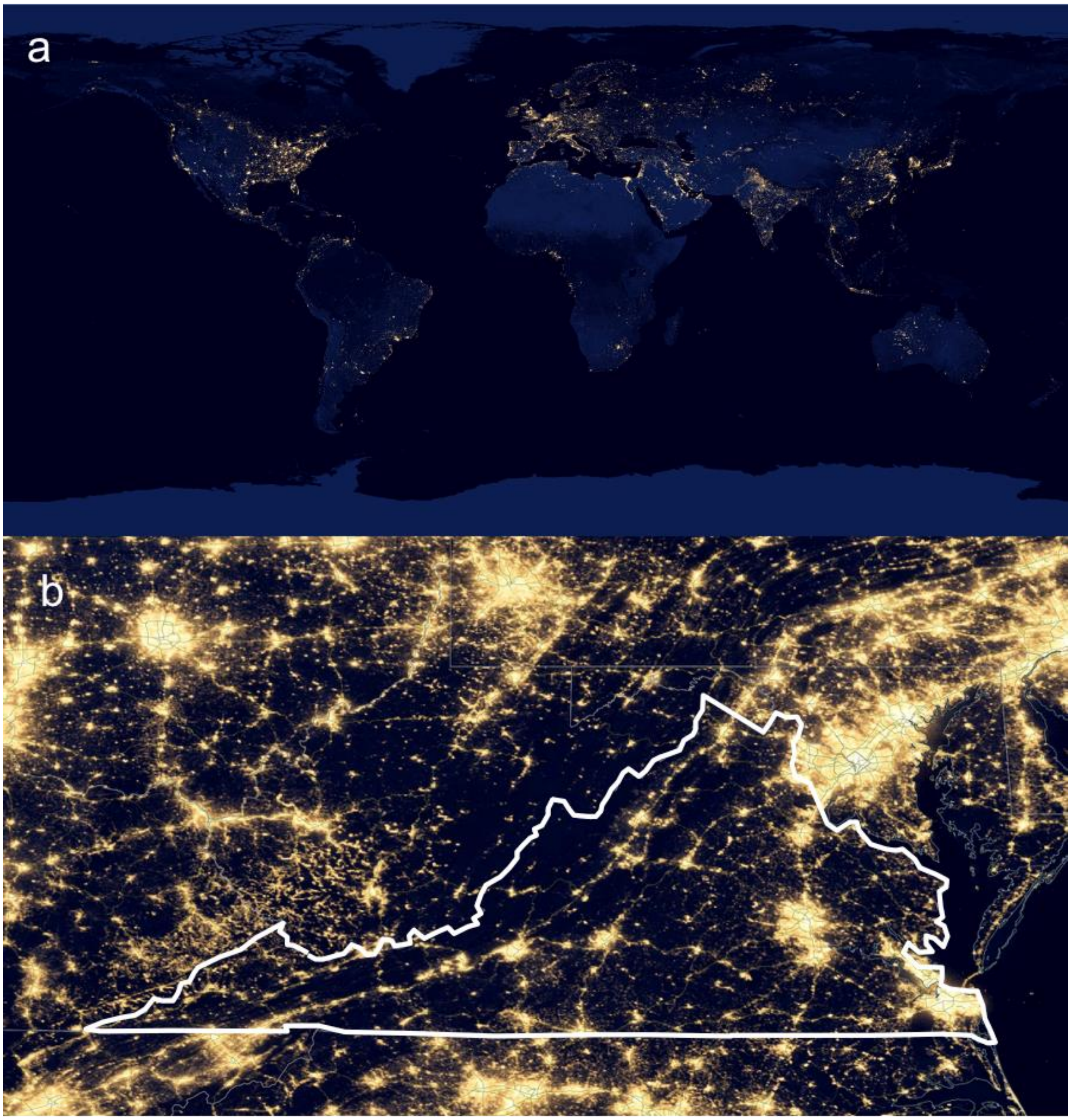

Figure 1. Satellite imagery of artificial light pollution in 2012 a) globally and b) in Virginia (VIIRS 2012; Elvidge *et al.* 2017).

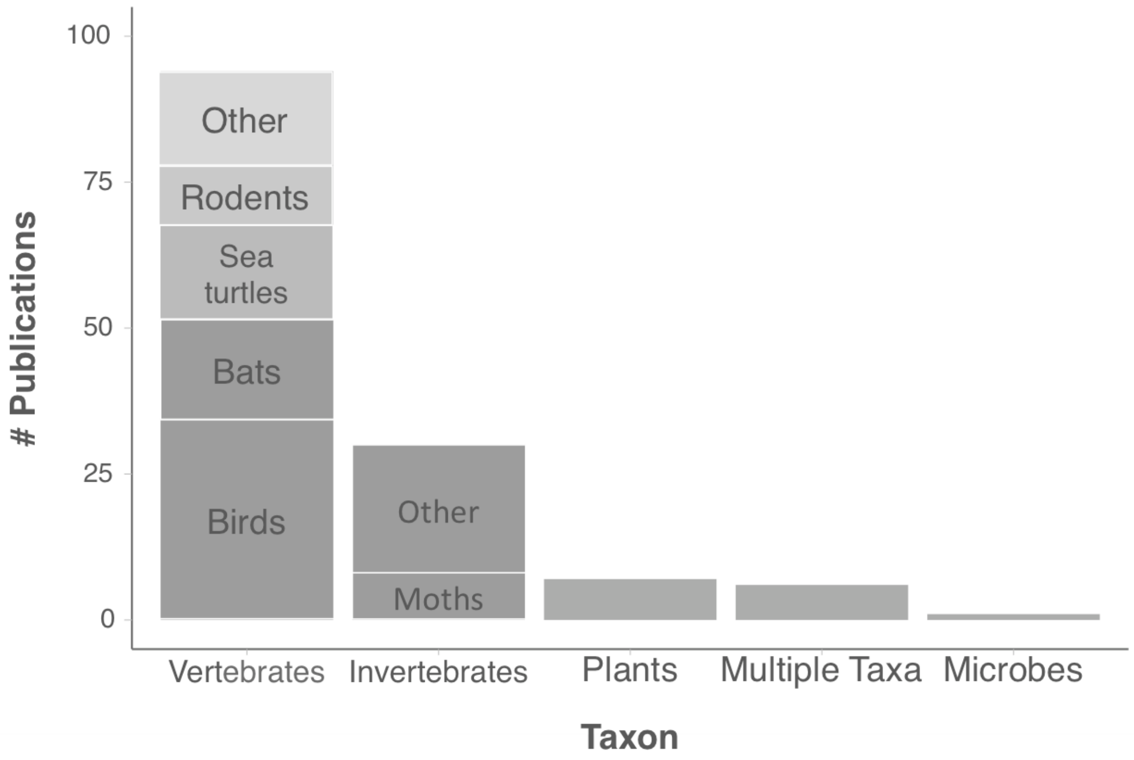

Figure 2. Number of publications about light pollution by taxonomic group. Records were from a Web of Science citation search for articles or proceedings papers in the science categories biology, ecology, or zoology published between 1970-2017 with the key terms “light pollution,” “artificial light at night,” “anthropogenic light pollution,” or “artificial night light*”. This search was conducted 12-15-17.

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Chapter 1

Experimental tests of light pollution impacts on nocturnal insect courtship and dispersal

Abstract

Though a number of effects of artificial light pollution on behavior and physiology have been described, there is little understanding of the consequences for the growth and distribution of populations. Here, I document impacts of light pollution on aspects of firefly population ecology and underlying mating behaviors. Many firefly species have a unique communication system where bioluminescent flashes are used in courtship displays to find and attract mates. I performed a series of manipulative field experiments in which I quantified the effects of adding artificial nighttime lighting on abundances and total flashing activity of fireflies, courtship behaviors and mating between tethered females and free-flying males, and dispersal distances of marked individuals. I show that light pollution reduces flashing activities in a dark-active firefly species (*Photuris versicolor*) by 70% and courtship behavior and mating success in a twilight-active species (*Photinus pyralis*). Though courtship behavior and mating success of *P. pyralis* was reduced by light pollution, I found no effects of light pollution on male dispersal in this species. My findings suggest light pollution is likely to adversely impact firefly populations and contribute to larger discussions about the ecological consequences of sensory pollution.

Introduction

Degradation of the sensory environment is a component of habitat loss. As land use intensification alters the structural landscape, the resulting spread of chemical, noise, and light pollution can affect habitat quality because of the impacts on the sensory information organisms use to interpret and interact with their surroundings (Francis & Barber 2013, Slabbekoorn *et al.* 2010, Longcore & Rich 2004, Scott & Sloman 2004). Artificial light at night erodes nighttime darkness, a potentially key component of habitat suitability for many species. Light pollution— defined here as illuminance from human activities— already envelops over 19% of the global land surface area and the affected area is increasing at a rate of 6% per year (Cinzano *et al.* 2001). The growing extent and severity of light pollution has effectively doubled the total surface brightness of the Earth at night from 1992-2012 (Elvidge *et al.* 2014). As light pollution spreads, understanding its ecological consequences is increasingly critical.

Light pollution is known to influence a range of biological activities (e.g., communication, movement; reviewed in Gaston & Bennie 2014, Gaston *et al.* 2014, Rich & Longcore 2006). Many organismal responses to light pollution—including phototaxis causing flying insects to circle lights to the point of exhaustion— are likely to influence demographic rates, in turn leading to impacts on abundance (Perkin *et al.* 2014, Frank 2006). However, the effects of light pollution at the population level remain unclear (Gaston & Bennie 2014). One problem is that many studies only report relationships between light pollution and species distributions or abundances without exploring the underlying causes.

Fireflies are an ideal study system for investigating how light pollution affects populations and the role of behavioral changes under field conditions. Many firefly species are nocturnal and use a visual communication system consisting of bioluminescent flashes to find and attract mates (Lloyd 1971). These courtship activities are sensitive to environmental light conditions. Flashing begins at or sometime after sunset when low ambient light levels enhance the contrast between the flash signal and the background environment (Lall *et al.* 1980), and the timing of nightly flashing activities can be advanced or delayed by natural variation in light levels due to cloud cover or the phase of the moon (Dreisig 1974, Allard 1931). The importance of light as a cue for firefly flashing has been corroborated by laboratory behavioral studies, which show that exposure to artificial light can stop or delay the timing of firefly flashing (Merritt *et al.* 2012, Dreisig 1975, Buck 1937, Rau 1932). These findings, combined with the observation that common lighting technologies overlap firefly flashes spectrally (Elvidge *et al.* 2010, Lall & Worthy 2001), have led to the hypothesis that light pollution may disrupt flash communication systems, with cascading effects on mating success and population persistence (Bauer *et al.* 2013, Faust *et al.* 2012, Lloyd 2006). Light pollution has been named a conservation threat for firefly populations worldwide (Bauer *et al.* 2013, Faust *et al.* 2012, Lloyd 2006); however, the effects of light pollution on populations are poorly understood.

Assuming a count of firefly flashes is a reasonable proxy of abundance, some studies contain evidence that light pollution affects firefly abundances and distributions. Hagen *et al.* (2015) observed reduced firefly activity when outside lighting was turned on, and Viviani *et al.* (2010) reported changes in firefly species composition across a spatial gradient in light levels. Picchi *et al.* (2014) observed *Luciola italia* fireflies less frequently in more light polluted areas of Turin, Italy as well as locations surrounded by a higher proportion of urban landcover. These surveys provide valuable observational survey data; however, given that light pollution is likely to increase with urban land cover (Small *et al.* 2005); experimental studies are needed to isolate effects of light pollution from other urban landscape characteristics.

In this study, I examined the effects of light pollution on the local abundances, dispersal, and mating activity of fireflies to inform inferences about population-level impacts. In one experiment, nighttime light pollution was manipulated in replicated experimental plots in a native plant meadow inhabited by two firefly species (*Photinus pyralis* and *Photuris versicolor*). Within these plots, I recorded counts of firefly flashes (a proxy for abundances) weekly over the course of a summer. In addition, to examine the potential importance of net movement away (repulsion) or toward (attraction) sources of artificial light, I conducted a mark-release-recapture study with *P. pyralis* males. I also investigated whether light pollution affects the mating behaviors and mating success of *P. pyralis*. I expected light pollution to cause local reductions in abundance due to net movement away (repulsion) from nighttime light sources. I also anticipated light pollution would reduce courtship activities and mating success.

Methods

Study organisms

Two species (*Photinus pyralis* and *Photuris versicolor*) dominate the firefly community at Blandy Experimental Farm (BEF), a University of Virginia environmental research station in the northern Shenandoah Valley of Virginia where this work was conducted (39°03′50.43″N, 78°03′47.20″W). *Photinus pyralis* is a common firefly species throughout eastern North America. Male *P. pyralis* display a characteristic “J-shaped” flight path while flashing. Females of *P. pyralis* are capable of flight over short distances, but perch on vegetation during nightly courtship activities (Lloyd 1966). *Photinus pyralis* flash courtship activities usually occur within 90 minutes of sunset at BEF. *Photuris versicolor* adults are predacious— luring prey firefly species (including *P. pyralis*) in to be eaten by mimicking their distinctive flash patterns (Lloyd 1980). At BEF, *P. versicolor* is most active 1-3 hours after sunset. *Photuris versicolor* flash patterns occur with a higher frequency than those of *P. pyralis* (Lloyd 1990), making it easy to differentiate between the two species based on their flash characteristics. In the following experiments, all applicable institutional and/or national guidelines for the care and use of animals were followed.

Flashing activities and abundances

A manipulative field experiment was conducted to examine the effects of light pollution on firefly flashing activities and abundances. I established eight experimental plots in May 2015 in a native grass meadow at BEF. Dominant vegetation within the plots included Indian grass (*Sorphastrum nutans*), switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*), musk thistle (*Carduus nutans*), wineberry (*Rubus phoenicolasius*), and milkweed (*Asclepias syriaca*). The plots were in fields with no other artificial lighting, and skyglow from human developments was low due to BEF's rural location.

The eight 20-m diameter plots were grouped into four pairs, with a 10 m edge-to-edge distance between plots in a pair and a minimum of 20 m between pairs. Within each pair, artificial light was added to one randomly chosen plot and the other plot, with no light added, served as a control. I erected wooden light posts in the center of each plot, including the control plots. At a height of 3 m, each light post was fitted with either four LED waterproof floodlights (RAB Lighting Bullet 12A) or a fake light fixture. I placed posts fitted with fake light fixtures in the control plots to avoid differences in physical structure between treatments because I observed that potential predators of fireflies (birds and spiders) frequently perched on the light posts in pilot studies. I chose LED lights because they overlap firefly flashes spectrally (Elvidge & Keith 2010, Lall & Worthy 2000), and because these technologies are becoming increasingly common in residential and commercial areas (Steele 2010). I chose a 10-m radius for the circular plots because this area could be effectively lit by the light fixtures, and was thought to be a relevant scale for firefly movement. A light sensor turned the floodlights on at dusk and off at dawn throughout the seasonal window of local adult firefly activity (mid-May through early August). I quantified illuminance within each plot at several distances from the plot center with a light meter (ExTech LT300) at a height of 1 m above the ground on a cloudless night with a new moon. To capture variation in illuminance due to the angle of the light sensor, light measurements were taken with the sensor pointed upward and with the sensor pointed directly at the light. Using the latter method, illuminance was 301.24 ± 89.07 (1 SD) lux at the center post in plots with artificial lights and 0.09 ± 0.10 lux in plots with no lights (Fig. 1).

Adult firefly flashes were observed one night each week from 8 June – 24 July. After 24 July, *P. pyralis* flash activity at BEF was 13% of peak and *P. versicolor* flash activity was 1.5% of peak. I measured the number of firefly flashes per minute in each plot at sunset, one hour after sunset, and two hours after sunset based on the mean of three one minute counts per time period. For each count, an observer stood at one of four cardinal directions around the plot periphery. Between each count, the observer either moved to a new, randomly selected location on the plot perimeter, or waited 30 seconds before beginning the next count in the event that the same location appeared consecutively in the random sequence. The purpose of moving randomly between counts was to ensure that the counts were not biased according to the location of the observer, for example due to obstructions presented by vegetation.

Visually surveying firefly flashes is a standard method for assessing local abundances (Takeda *et al.* 2006, Cratsley & Lewis 2005, Lewis & Wang 1991, Yuma & Ono 1985, Hori *et al.* 1978). I tested the assumption that differences in the rate of firefly flashing (e.g., flashes per minute) among locations reflect differences in abundance by comparing visual counts of flashes with a non-visual measure of firefly abundances. Two concerns motivated this test. First, differences in the rate of flashing among plots might be influenced by the propensity of individuals to flash as well as firefly abundance. Second, it is plausible that firefly flashes may be easier for researchers to detect in darker locations due to the higher contrast between the flashes and the background. For my non-visual method, I completed sweep net samples of all of the non- *Rubus* vegetation (~20% of the area in each of two paired plots) within each plot at waist level three times during the summer. Plots were sampled at sunset and one hour after sunset. Fireflies were released back into the plots where they were captured at the end of sampling each night. I decided to use sweep net sampling instead of LED firefly traps (Bird & Parker 2014, Woods *et al.* 2007) as a non-visual abundance metric to avoid destructively sampling the population, and because my experimental manipulation of light levels could conceivably affect the attractiveness of the LED lure (Bird & Parker 2014).

As ambient light levels decreased over the course of each evening, it became increasingly difficult for researchers to see the plot boundaries. To ensure firefly flashes were counted within a standard area in both treatments, I marked plot boundaries with blue, chemiluminescent glow sticks before each survey. Fireflies may be insensitive to blue wavelengths of light (Lall & Worthy 2000), and the presence of glow sticks did not change light levels at the plot boundaries by more than 0.01 lux, the minimum illuminance detectable by my light meter.

To test the effects of light pollution on the flash activity of a given species (*P. pyralis or P. versicolor*) over the course of the summer, I used a generalized linear mixed model (GLMM) with light pollution, week, and light pollution × week interaction as fixed effects, and plot pair as a random effect. The dependent variable was the mean of the number of firefly flashes per minute. I specified a Poisson distribution for the dependent variable and log link function. To test whether effects of light pollution on firefly flash activities changed with time of night for a given species, I used a GLMM with light pollution, observation round (i.e. sunset, one hour after sunset, two hours after sunset), and light pollution × observation round as fixed effects, and plot pair as a random effect. As before, I specified a Poisson distribution for the dependent variable with a log link function. All statistical analyses were conducted using SAS software (SAS Institute, Inc. Cary, NC, USA).

I also tested the assumption that firefly flash counts are a reasonable proxy of local abundances by evaluating the relationship between the mean number of *P. pyralis* flashes per minute over the course of the summer and the number of *P. pyralis* captured using a Pearson correlation. Both variables were log-transformed to meet the assumptions of the test. These data were pooled across all sample periods due to low overall numbers of captured individuals. Sweep net capture of the second firefly species, *P. versicolor*, was too low to analyze statistically.

Mating behaviors and mating success

To assess how light pollution affects *P. pyralis* mating behavior, I observed courtship dialogues between free-flying males and tethered female *P. pyralis* in the field with and without artificial lighting between sunset and 2 hours after sunset (20:30-22:30). The study was conducted in a native grass meadow that was continuous, but 200 m away, from the meadow containing the plots for the local abundances experiment. Female tethering locations were grouped in pairs with a distance of 20-30 m between points within a pair. I randomly assigned one point within a pair to receive light pollution. The light pollution treatment consisted of two LED floodlights (Ultra-Tow 9-32 Volt LED Floodlight) mounted to a post at a height of 3 m with a mean illuminance of 167.21 ± 1.61 (1 SD) lux. Lights were powered with 12V, 35 amp batteries. Because researchers trampled some of the vegetation while setting up the light fixtures, I also walked around the control points several times to similarly disturb plots in both treatments.

I collected female *P. pyralis* for the experiment at BEF within 24 hours of each trial. I tethered each female to a perch consisting of a 4 × 20 cm wooden platform on top of a 0.5 m garden stake just prior to twilight and the onset of firefly activity. Perches were positioned 2 m away from the light post or control point. A 30-cm length of cotton sewing thread was looped around a joint between the female's pronotum and abdomen to form a noose, with the leading end of the noose positioned dorsally. Females could walk normally while tethered.

A female was allowed to acclimate for 5 minutes before the observation period began. I then observed each female continuously for 15 minutes. The observer sat 2 m away from each tethered female and recorded several metrics of mating activity: the number times the female flashed, the number of males flying within 1 m of the female, and the number of times males within 1 m of the female flashed. I carried out 27 replicate mating trials for each treatment, observing a unique female in every trial.

Differences in mating behavior metrics were assessed with a MANOVA, with light treatment as a fixed effect and pair as a random effect. All of the response variables were log-transformed to improve normality and homogeneity of variance. Following the finding of a significant multivariate response, univariate ANOVAs were also performed using each of the response variables (Quinn & Keuogh 2002).

Dispersal

To study whether fireflies tend to move towards or away from artificial lights, I released marked male *P. pyralis* fireflies in plots with light pollution added and control plots with no added light and monitored firefly displacement from the release point. Again, I used *P. pyralis* instead of *P. versicolor* in this experiment for logistical reasons. *Photinus pyralis* was more abundant than *P. versicolor* at BEF, and I was unable to capture *P. versicolor* in sufficient numbers for a mark release recapture experiment. Paired release sites were established in lawn areas at BEF, with 80 m between paired release sites and at least 300 m between pairs of release sites. Light pollution treatment levels (light polluted or control) were randomly assigned to the points within each pair. Light pollution was added with two LED floodlights mounted to a post at a height of 3 m, with a mean illuminance of 167.21 ± 1.61 (1 SD) lux. LED lights were turned on dusk to dawn during the experiment. A barrier (i.e. road, hill crest, clump of trees) always separated the light pollution treatment and control release points so that they were never within eyesight of each other.

Males of *P. pyralis* fireflies were captured at night 24 hours prior to the release, marked with fluorescent powder, and housed in outdoor containers. At sunset the following evening, I released 100 males at each point within a pair, using a different color of marking for each point. In a single night, releases were carried out in 1-2 plot pairs. Twenty-four hours after a release, all live *P. pyralis* fireflies were recaptured within two distance ranges from each release point: 0-8 m and 8-16 m. Pilot studies showed that attempting to recapture at farther distances was too time consuming to complete within the short nightly activity period of *P. pyralis*. The time spent collecting within each distance section (7 minutes 30 seconds in the inner section, 22 minutes 30 seconds in the outer section) was adjusted based on the area of that section to standardize the sampling effort. Paired plots were sampled by two persons simultaneously (one collector per plot). The collectors switched plots halfway through the sampling period to correct for potential differences in sampling efficiency between individuals.

The collectors typically caught all of the fireflies that were visible in a particular distance range before the sampling time period ended. For this reason, I judged that standardizing the number of recaptures by the area searched (201.6 m^2 or 603.19 m^2) was the least biased estimator of recaptures. To test for effects of light pollution on firefly displacement from the release point, I used a GLMM with light pollution, recapture distance, and the light pollution × recapture distance interaction as fixed effects and pair and plot as random effects. The response variable was the number of marked fireflies recaptured /m^2. This was square-root transformed to meet normality and homogeneity of variance assumptions. The prediction that light pollution affected displacement distance was tested based on the light pollution × recapture distance interaction. In the process of recapturing marked fireflies, collectors also captured unmarked fireflies. I tested effects of light pollution on the distribution of the unmarked fireflies (males $\text{captured}^{0.5}/m^2$) with a second GLMM with the same fixed and random effects as the previous model.

Results

Flashing activities and abundances

I counted a total of 10,699 and 903 *P. pyralis* and *P. versicolor* flashes, respectively, over the course of the seven weeks of this experiment. The median number of flashes observed per minute was 22.29 for *P. pyralis* and 1.88 for *P. versicolor*.

Light treatment did not significantly explain differences in the mean number of *P. pyralis* flashes per minute over the seven weeks of the experiment (Fig. 2). For this species, flash activity peaked in week 4 of the study, and week explained a significant portion of the variation in flash counts (Table 1). Within nights, the greatest number of *P. pyralis* flashes was observed at sunset, but light pollution neither delayed nor advanced the timing of *P. pyralis* activity (Table 1).

Light pollution strongly affected mean *P. versicolor* flashes per minute, reducing the number of *P. versicolor* flashes observed in the control plots by 69.69% compared to the light polluted plots (Fig. 2). *P. versicolor* flash counts peaked in week 1 of the study. Week explained a significant portion of the variation in flash counts, but there was not a significant week × light pollution interaction (Table 1).Within nights, there was not a significant effect of observation round (i.e. sunset, 1 hour after sunset, 2 hours after sunset) on *P. versicolor* flash counts (Table 1).

The mean number of *P. pyralis* flashes observed per minute in each plot over the course of the summer was positively correlated with the total number *of P. pyralis* ($r = 0.77$, $n = 8$, $P = 0.025$) and the number of male *P. pyralis* (Fig. 3, $r = 0.78$, $n = 8$, $P = 0.020$) captured in sweep net surveys (all variables log transformed). As I found with the flash count surveys, there was no significant difference in total number of male *P. pyralis* captured between light pollution treatment levels (Paired t-test, $P = 0.72$, $t = 0.39$, $df = 3$).

Mating behaviors and mating success

On average, 4.10 male *P. pyralis* flew within 1 m of each tethered female during the 15 minute observation periods. Ninety-four percent of males flashed at least once. The median number of flashes observed per male was 3. Forty-three percent of tethered females flashed at least once. Among females who flashed, the median number of flashes was 2.

Based on a MANOVA, I found a multivariate effect of light pollution on *P. pyralis* mating behavior (Wilks' $\lambda = 0.814$, $F_{4,51} = 2.89$, $P = 0.031$). Univariate ANOVAs of each of the response variables revealed that females were 3 times more likely to flash in the control treatment (Fig. 4a; $F_{1,54} = 6.84$, $P = 0.012$). There was no significant difference in the number of males flying within 1 m of the female (Fig. 4a; $F_{1,54} = 1.30$, $P = 0.26$), or the proportion of those males that flashed (Fig. 4b; $F_{1,54} = 2.10$, $P = 0.15$).

Five females mated with males during the observation periods and reached the stage of copulation in which spermatophore transfer occurs (Lewis & Wang 1991). All females that mated were in the control treatment.

Dispersal

I recaptured 237 out of 2,000 marked *P. pyralis*, or roughly 12% of those released. Recapture rates ranged from 1-44%, with a mean of 11.92% ± 9.75 (1 SD). There was no significant effect of light pollution treatment on displacement distance (light pollution × distance; Fig. 5a; $F_{1,18} = 0.16$, $P = 0.69$). I also captured 1,613 unmarked *P. pyralis* while sampling during the course of the experiment. There was no significant effect of light pollution on the mean number of unmarked fireflies captured ($F_{1,18} = 0.29$, $P = 0.60$; Fig. 5b), nor was the light pollution × distance interaction significant ($F_{1,18} = 0.17$, $P = 0.21$).

Discussion

To date, research on the ecological consequences of light pollution has focused mainly on organism-level effects such as changes in physiology or behavior, with little focus on the implications for populations (Gaston & Bennie 2014). Few studies have demonstrated impacts on species abundances or distributions with controlled experiments. One notable exception is van Geffen *et al.* (2015), who showed that LED lights reduced mating success in a geometrid moth. Here I report on some of the first experimental testing of effects of light pollution on local abundance, as well as mechanisms (dispersal and mating success) potentially influencing abundance.

I demonstrated that light pollution disrupts female firefly courtship flashes (Fig. 4a) and mating success (mating only occurred in control plots), which may in turn lead to reduced rates of reproduction and population growth in light-polluted areas. The reduction in mating success appeared to be driven by changes in the behavior of females rather than males. Males of *P. pyralis* were no less active or abundant in light-polluted plots, and my dispersal experiment results produced no evidence of males being attracted to, or repelled by, artificial light. While the continued courtship activity of *P. pyralis* in light polluted conditions appears counterproductive given that no mating occurred, the fact that males were not attracted towards the artificial lighting may limit the impacts of light pollution on *P. pyralis* populations to light polluted areas. The lack of attraction to artificial lighting in fireflies is in contrast to species attracted to artificial light (e.g., some moths, beetles, and aquatic insects; Eisenbeis 2006, Perkin *et al.* 2014), where aggregation in light-polluted areas could create population sinks. Studies that document spatial (immigration and emigration) as well as non-spatial components (births and deaths) of demography will be most informative for inferring population-level impacts of light pollution.

Perhaps uniquely, I use two methods to assess firefly abundances: visual counts of firefly flashes and sweep net capture. I found that the number of individuals collected during sweep net capture was positively correlated with flashes per minute, suggesting visual surveys of firefly flashes are a reasonable proxy for *P. pyralis* abundances. When possible, I recommend non-visual surveys should be used to complement visual surveys when measuring firefly abundances. The combination of flash counts and sweep net surveys allows us to conclude the local abundance of *P. pyralis* was not affected by light pollution over the span of a single adult generation. However, it is important to consider that effects on abundance might arise over a longer timeframe if the observed reduction in mating success inhibits reproduction.

My finding that light pollution did not affect male *P. pyralis* abundances near tethered females contrasts with Bird and Parker's (2014) observation that males of *Lampyris noctiluca*, a European firefly species, were less attracted to simulated females in the presence of light pollution. Previous laboratory work with *L. noctiluca* also shows that artificial light decreases female bioluminescent activity (Dreisig 1978), a finding echoed in my study with *P. pyralis* females. Despite the different responses of *L. noctiluca* and *P. pyralis* males, and although female bioluminescence behaviors differ for these two species— *L. noctiluca* females produce a continuous glow while *P. pyralis* females produce discrete flashes— light pollution may have a similarly negative impact on mating success in these two species.

I expect a reduction in courtship dialogues may have complex effects on individual fitness in *P. pyralis*. In many firefly species (including *P. pyralis*), females mate multiple times and gain supplemental resources with each additional mating in the form of a male nuptial gift (van der Reijden *et al.* 1997, Lewis *et al.* 2004). The fitness pay-off of mating multiple times, and penalty of failing to do so, may be particularly large in this system because *P. pyralis* do not eat as adults. My findings suggest future avenues of research exploring the effects of light pollution on *P. pyralis* fecundity, and in turn, on the growth and dynamics of firefly populations in affected areas.

In contrast to *P. pyralis*, light pollution resulted in decreased flashing activity in *P. versicolor*. *Photinus pyralis* is generally active earlier in the evening than *P. versicolor* when natural light levels are higher, but are rapidly decreasing. Divergent responses to light pollution among twilight- and dark-active fireflies may reflect differences in the ability of these species to tolerate diverse light conditions, or the fact that ambient light levels are simply higher earlier in the evening and may already exceed light levels from artificial light illumination. In other systems, light pollution has also been found to affect nocturnal species more strongly than crepuscular species (Azam *et al.* 2015, Rotics *et al.* 2011). Temporal niche may be an important trait influencing how a species will respond to light pollution.

My observation that light pollution reduces firefly mating opportunities joins a chorus of other examples of communication systems disrupted by sensory pollution. Acoustic pollution has been shown to alter signal characteristics and behavior in birds (Slabbekoorn 2013, Proppe *et al.* 2013), crickets (Costello & Symes 2014), whales (Miller *et al.* 2000), and frogs (Bee & Swanson 2007). Nutrient pollution reduces the efficacy of a colored sexual display in sticklebacks (Wong *et al.* 2007, Candolin *et al.* 2007). Atmospheric pollutants can degrade plant volatiles (McFrederick *et al.* 2008, Girling *et al.* 2013), with the potential for cascading effects on the networks of pollinators and herbivores that depend on them. Because communication often plays a role in mate-finding and assessment, there is a clear need to explore the implications of sensory pollution for individual fitness and demographic processes separate from other stressors than may occur in human-modified landscapes.

I show that anthropogenic disturbance in the form of light pollution reduces flash activities in a dark-active firefly species and mating success in a twilight-active species. These results suggest that light pollution has the potential to adversely affect firefly populations, and point to the need for additional work on the effects of increasing urbanization of landscapes on mating behavior and the fallout for population persistence. In the case of *P. pyralis* populations, adverse effects of light pollution would not have been noticed if my inferences were based solely on abundances and reductions in mating success had not been detected.

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Tables & Figures

Table 1. Results of generalized mixed models testing the effects of light pollution on firefly flashing activity and abundance.

Species	**Variable**	F_{df}		p
P. pyralis	week	$F_{6,42}$	3.24	0.011*
	light pollution	$F_{1,6}$	1.75	0.23
	week × light pollution	$F_{6,36}$	0.16	0.99
	observation round	$F_{2,6}$	55.38	≤ 0.01**
	observation round x light pollution	$F_{2,6}$	0.54	0.61
P. versicolor	week	$F_{6,36}$	2.37	0.05*
	light pollution	$F_{1,6}$	10.55	0.02*
	week × light pollution	$F_{6,36}$	0.31	0.93
	observation round	$F_{2,6}$	2.04	0.21

* denotes a result that is significant at the $\alpha = 0.05$ confidence level

** denotes a result that is significant at the $\alpha = 0.01$ confidence level.

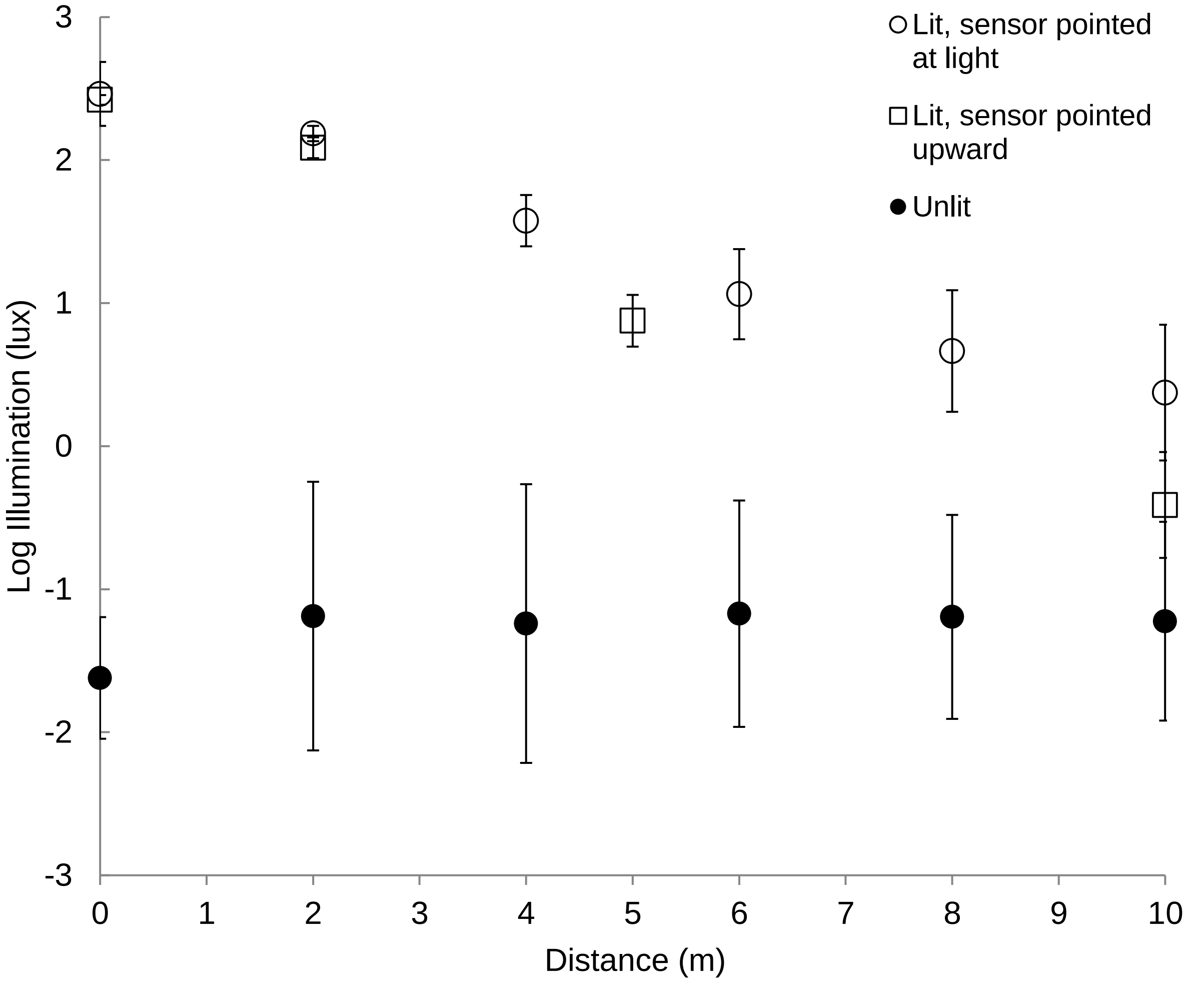

Figure 1**.** Illumination (lux) in the experimental plots used for the firefly abundance experiment. Light levels were measured with the light sensor angled towards the artificial light and with the light sensor angled directly towards the sky. Data are means ± 95% CI.

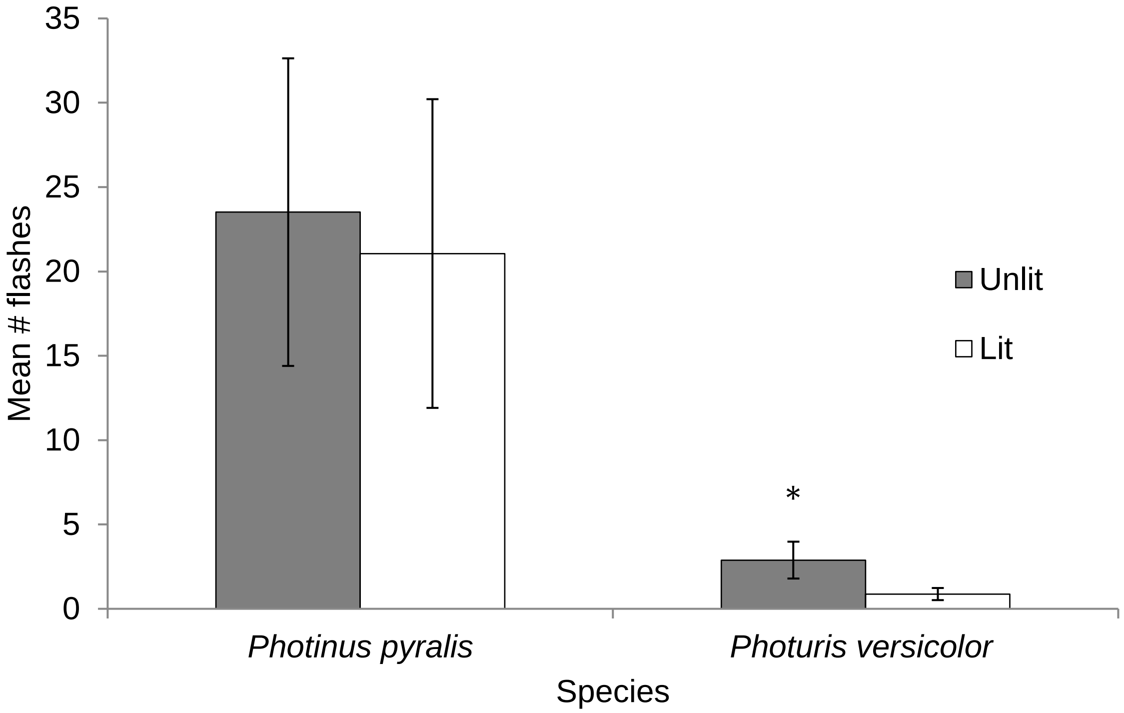

Figure 2. The effect of light pollution on the number of *P. pyralis* and *P. versicolor* flashes per minute in the flashing activity and abundance experiment (GLMM, statistical results in Table 1). The nightly mean number of flashes per minute was calculated for each plot by taking the average of three one-minute observations made at sunset, one hour after sunset, and two hours after sunset. Nightly means were then averaged across the seven weeks of the study. Data are means ± 95% CI. * denotes a statistically significant finding at the α = 0.05 confidence level.

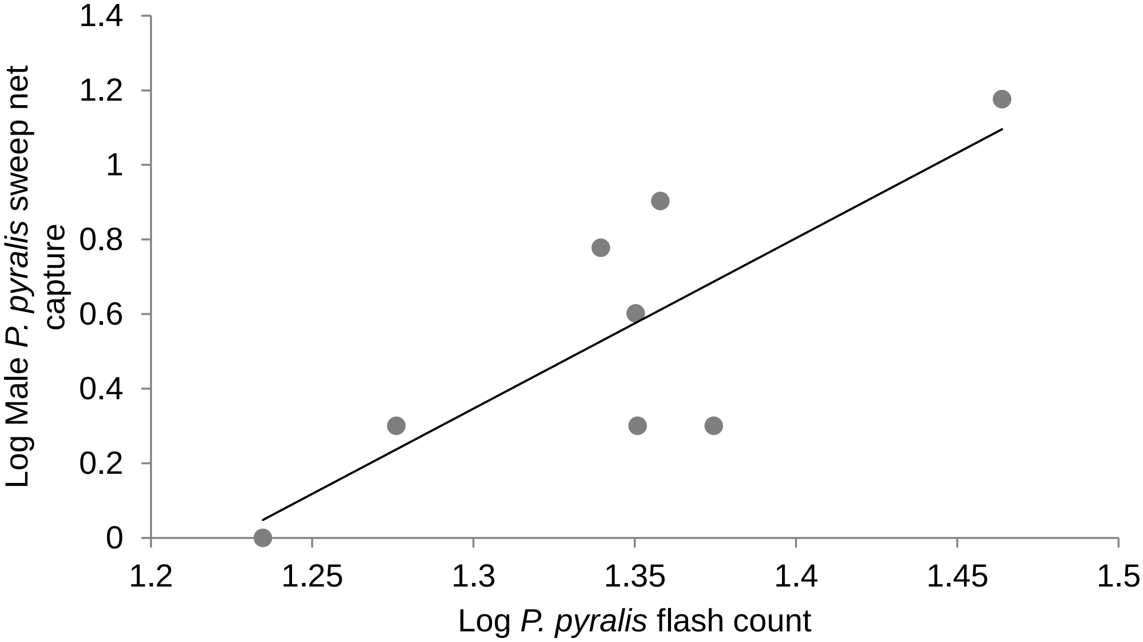

Figure 3. Scatterplot and trend line of the relationship between the mean number of flashes observed in each plot over the course of the summer and the number of male *P. pyralis* captured in sweep net surveys (both log transformed; $r = 0.78$, $n = 8$, $P = 0.020$).

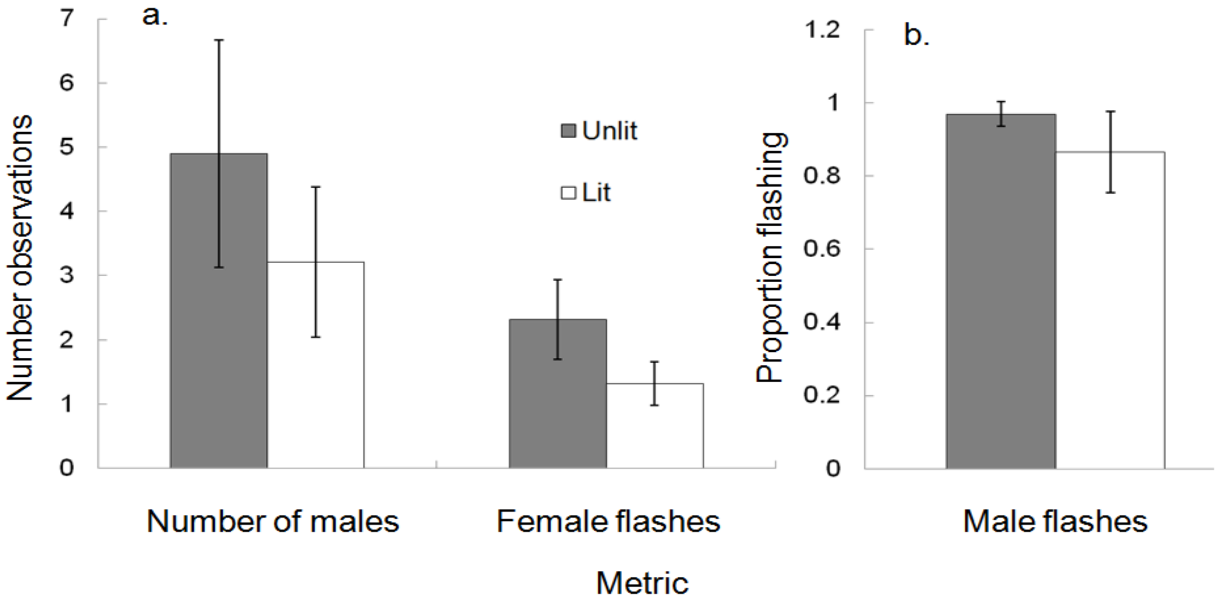

Figure 4. Effect of light pollution on a) male *P. pyralis* abundances (ANOVA, $F_{1,54} = 1.30$, $P = 0.26$) around tethered females and number of female response flashes (ANOVA, $F_{1,54} = 6.84$, $P = 0.012$) and b) proportion of male *P. pyralis* that flashed within 1 m of a tethered female (ANOVA, $F_{1,54} = 2.10$, $P = 0.15$). Data are means ± 95% CI. * denotes a statistically significant finding at the $\alpha = 0.05$ confidence level.

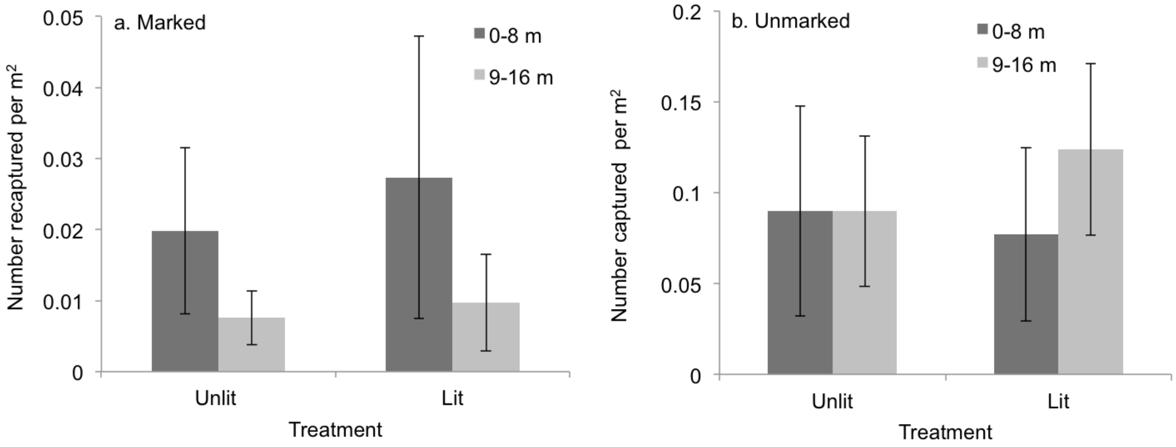

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Figure 5a). Effect of light pollution on male *P. pyralis* dispersal (GLMM, $F_{1,18}$ = 0.16, P = 0.69). Fireflies were either released directly under a light source (light pollution treatment) or at a point with no light source (control). Darker grey bars represent the number recaptured per minute 0-8 m from the release point and lighter grey bars represent the number recaptured 9-16 m from the release point. b) Effect of light pollution on captures of unmarked *P. pyralis* (GLMM, $F_{1,18}$ = 0.17, P = 0.21). Data are means ± 95% CI.

Chapter 2

Light pollution may create demographic traps for nocturnal insects

Abstract

Light pollution impacts both intra- and inter-specific interactions, such as interactions between mates and predator-prey interactions. In mobile organisms attracted to artificial lights, the effect of light pollution on these interactions should be intensified. If organisms are repelled by artificial lights, effects of light pollution on intra- and inter-specific interactions should be diminished as organisms move away. However, organisms repelled by artificial lights would likely lose suitable habitat as light pollution expands. Thus, I need to understand how light pollution affects both net attraction or repulsion of organisms and effects on intra- and inter-specific interactions. In manipulative field studies using fireflies, I found that *Photuris versicolor* and *Photinus pyralis* fireflies were lured to artificial (LED) light at night and that both species were less likely to engage in courtship dialogues (bioluminescent flashing) in light polluted field plots. Light pollution also lowered the mating success of *P. pyralis*. *Photuris versicolor* is known to prey upon *P. pyralis* by mimicking the flash patterns of *P. pyralis*, but I did not find an effect of light pollution on *Photuris-Photinus* predator-prey interactions. Light pollution is growing in spatial extent and severity, but impacts on insect populations are poorly understood. My study suggests that for some nocturnal insects light polluted areas may act as demographic traps, *i.e.*, areas where immigration exceeds emigration and inhibition of courtship dialogues and mating reduces reproduction. Examining multiple factors affecting population growth in concert is needed to understand and mitigate impacts of light pollution on wildlife.

Introduction

Human land use changes (*e.g.*, urbanization and agricultural intensification) affect large swaths of the globe (Venter *et al.* 2016), and are considered major drivers of biodiversity loss (Foley *et al.* 2005, Newbold *et al.* 2015). One component of land use change is alteration of sensory inputs: new photic, acoustic, tactile, and olfactory regimes (*i.e.*, sensory pollution; (Halfwerk and Slabbekoorn 2015). Because organisms use sensory information to interpret and interact with their surroundings, sensory pollution is increasingly recognized as a conservation concern, especially in cases where the organism's response decreases fitness (Delhey and Peters 2017). Light pollution— defined here as artificial illuminance — alters visual information for crepuscular and nocturnal organisms (Davies *et al.* 2013b). Light pollution already covers over 22.5% of the global land surface area (Falchi *et al.* 2016b), and Cinzano *et al.* (2001) showed that light pollution is increasing spatially at a rate of 6% per year. As light pollution spreads, understanding its ecological consequences is increasingly critical.

Impacts of light pollution on intra-specific interactions are largely unexplored (Longcore and Rich 2004), but one area where they do seem to be important is sexual behavior (Delhey and Peters 2017). For example, misleading light cues from artificial light could disrupt the release of reproductive hormones (Russ *et al.* 2015), pheromone signaling (van Geffen, van Eck, & de Boer, 2015), or courtship behaviors prior to mating (Endler 1992, Endler and Thery 1996, Heindl and Winkler 2003). Botha *et al.* (2017) show light pollution effects on sexual behavior are complex; lifetime exposure to elevated light conditions in the lab increased male cricket mating probability, decreased female cricket precopulatory behaviors associated with mating efficiency, and had no effect on the number or structure of acoustic courtship calls. Light pollution could also impact reproduction indirectly by affecting movement behaviors that determine the spatial aggregation of conspecific individuals. There is evidence attraction to artificial lights is sex-dependent in some moth species (Altermatt *et al.* 2016, Degen *et al.* 2016), but the effects on mating of attraction to artificial lights remain unknown.

Light pollution may also impact inter-specific interactions (Longcore and Rich 2004). For example, attraction to or repulsion from artificial lights may alter encounter rates between predators and prey. Minnaar *et al.* (2015) found moth consumption by bats increased near lights despite lower relative moth abundances in lit areas. Rydell (1991) showed predators adjust the areas over which they forage in response to light-mediated changes in prey availability. Conversely, prey behavior may change if predation risk in artificially lit areas is heightened or is perceived to be heightened. Yorzinski *et al.* (2015) observed peahens increased anti-predator vigilance behaviors under artificial lights, and Rotics *et al.* (2011) found one mouse species spent less time performing conspicuous activities under lights. Additionally, light from the full moon is known to increase prey anti-predator or vigilance behaviors (Beauchamp and McNeil 2003, Biebouw and Blumstein 2003, Kotler *et al.* 2010). By giving advantage to a predator or its prey (or vice versa), light pollution could potentially destabilize predator-prey interactions.

Few studies have examined effects of light pollution on predator prey interactions in invertebrates. Bennie *et al.* (2015) found no interactive effect of light pollution and predator presence on aphid abundance experimental mesocosms. Underwood *et al.* (2017) showed dogwhelk mollusks acclimated to light pollution were more likely to engage in conspicuous foraging activities in the presence of olfactory predator cues. Miller *et al.* (2017) showed light pollution decreased aphid consumption by one nocturnal ladybug species that used visual cues to find prey, but had no effect on aphid consumption by another nocturnal ladybug species that used non-visual cues to find prey. While some predator species may exploit lights to their advantage, other predator species may be negatively impacted.

Fireflies are ideal for studying effects of light pollution on intra- and inter-specific interactions due to their unique, light-based communication system used for both courtship and predation (many predaceous species lure in prey species by mimicking their flash patterns; (Lloyd, 1975). Fireflies are beetles in the family Lampyridae, There are about 2,000 species described worldwide, and they occur on almost every continent (Lloyd, 2004). Many firefly species are nocturnal or crepuscular and communicate using bioluminescent flashes. Laboratory experiments have shown artificial light can stop or delay the timing of firefly flashing (Buck 1937, Merritt *et al.* 2012). Observational field studies have reported reduced nocturnal firefly flashing in light polluted areas (Hagen *et al.* 2015; Picchi *et al.* 2013; Viviani *et al.* 2010). Additionally, manipulative experiments showed light pollution reduced bioluminescent courtship signaling (Bird and Parker, 2014; Firebaugh and Haynes, 2016). The effects of light pollution on predator-prey interactions between firefly species have not been evaluated. In addition, the effects of light pollution on firefly movement (attraction or repulsion from artificial lights) is also poorly understood (Firebaugh and Haynes, 2016).

I conducted a series of field experiments to examine effects of light pollution on intra-specific (courtship) interactions in *Photuris versicolor* fireflies and inter-specific (predator-prey) interactions between *P. versicolor* and *Photinus pyralis.* I also investigated whether these species displayed net movement towards (attraction) or away (repulsion) from artificial lights at night. Previously, *P. pyralis* females were shown to flash three times less frequently in the presence of artificial lights (Firebaugh and Haynes, 2016), but effects on *P. versicolor* courtship were not studied. To assess how light pollution impacts *P. versicolor* mating behavior, I observed courtship dialogues in the field with and without artificial lighting. To explore interactions between light pollution, predator-prey interactions, and prey mating behaviors, I conducted a manipulative experiment where the prey species (*P. pyralis*) and was exposed to light pollution or natural light conditions with and without the predator species (*P. versicolor*) present. I predicted light pollution would decrease *P. versicolor* flashes based on a previous finding of reduced flashing activity in experimentally lit portions of a field (Firebaugh and Haynes 2016). I also predicted the presence of a predatory firefly (*P. versicolor*) would reduce *P. pyralis* flashing as courtship flashing may make *P. pyralis* more vulnerable to predators.

Methods

Study system

Firefly flashes enable species identification during courtship. Male fireflies flash with a species-specific flash pattern, and conspecific females respond by flashing back (Lloyd, 1971). Flashing begins at or soon after sunset when ambient light levels are low (Lall *et al.*1980). In addition to their role in courtship, firefly flashes play a role in predator-prey interactions between predatory fireflies in the genus *Photuris* and *Photinus* fireflies. *Photuris* males and females mimic the flash patterns of *Photinus* prey to lure in *Photinus* fireflies (Lloyd, 1981). Predation of *Photinus* fireflies allows *Photuris* fireflies to accumulate lucibufagin compounds, which make them distasteful to generalist predators (Eisner *et al.* 1997).

This study was conducted during the summer of 2016 at Blandy Experimental Farm (BEF), a University of Virginia research station (39°03′50.43″N,78°03′47.20″W). *Photinus pyralis* and *Photuris versicolor* dominate the firefly community at BEF. *Photinus pyralis* is a common firefly species throughout eastern North America (Lloyd, 2004). At BEF, *P. pyralis* courtship displays usually occur within 90 minutes of sunset at BEF, whereas *P. versicolor* is most active in courtship displays1-3 hours after sunset. *Photuris versicolor* flash patterns are more rapid than those of *P. pyralis* (Lloyd, 1990), making it easy to differentiate between the two species.

Photuris versicolor courtship

To assess how light pollution affects *P. versicolor* mating behavior, I observed courtship dialogues between free-flying males and stationary females in the field with and without artificial lighting. I placed female *P. versicolor* in 10 × 10 × 10 cm nylon mesh containers. The bottom of the container was open so the females could sit on vegetation (warm-season grasses), as they normally do during courtship activities (Lloyd 2004). Females were given 10 minutes to acclimate to the cage before I began recording behavior. I observed each female for 15 minutes, and recorded the number of flashing *P. versicolor* males within 1 m of the female, and the number of flashes from the caged female. Plots were paired with a distance of 20 m between plots within a pair. The light pollution treatment, consisting of 2 downward pointing white LED floodlights (Ultra-Tow 9-32 Volt LED Floodlight, Northern Tool & Equipment Company, Inc., Burnsville, Minnesota, USA) mounted at a height of 3 m, was randomly assigned to one plot within each pair. Mean illuminance at chest height directly under the light fixture at plots receiving the light pollution treatment was 57.4 ± 0.89 lux, comparable to illuminance on a bright urban street (Gasto *et al.*, 2014). Mean illuminance at unlit plots was 0.03 ± 0.01 lux. Trials took place from 9:30-11:30 PM over the course of 10 nights in June.

Effects of light pollution on male *P. versicolor* flash activity were analyzed using linear mixed effects (LME) models (Bates *et al.* 2015), with light pollution as a fixed effect and observation pair as a random effect. The number of male flashes per minute was log transformed to improve the normality of the LME model residuals. For females, lack of variability in the rate of flashing in the light pollution treatment (see Results) prevented statistical analysis.

Predator-prey interactions and prey mating behaviors

I conducted a manipulative field experiment to examine effects of light pollution on predation of *P. pyralis* by *P. versicolor* and to assess whether *P. pyralis* altered its rate of courtship flashing in response to presence of the predator species under dark or artificially lit conditions. The experiment was conducted in four 3 × 3 × 3 m floorless, mesh-sided tents (Caravan Canopy, Caravan® Global US, La Mirada CA) placed over mowed vegetation in an old field meadow. I stocked all mesocosms with 3 males and 1 female *P. pyralis*.

Light pollution (present or unlit control) and predator density (one female *P. versicolor* or no predators) treatments were applied to the mesocosms according to a factorial design with 14 replicate trials. Light pollution was added by mounting 1 LED light (Ultra-Tow 9-32 Volt LED Floodlight) in the center of a mesocosm at a height of 2.5 m. Light intensity at chest height in mesocosms with artificial light added measured 174.53 ± 1.08 lux. Light intensity in unlit cages was 0.03 ± 0.02 lux. Each trial took place over approximately 7 hours (17:00-24:00). *Photuris versicolor* and *P. pyralis* densities (no. per m^{-2}) in the experiment were approximately one third and one fifth, respectively, the peak densities observed at BEF in 2015 (Firebaugh and Haynes, 2016).

Fireflies were marked with fluorescent powder to facilitate recapture, and were put in the mesocosms at 5:00 PM before each trail. I counted the number of flashes during three one minute counts by male and female *P. pyralis* and female *P. versicolor* in each tent at sunset, one hour after sunset, and two hours after sunset. Each trial lasted 1 night. After the final observation round, I recovered all fireflies and recorded the number living and dead. A UV flashlight was used to recover the fireflies (the fluorescent powder glowed under UV light). I determined whether *P. pyralis* females had mated by checking their genitalia for the presence of the fluorescent powder color used to mark *P. pyralis* males.

Effects of light pollution and predator presence on *P. pyralis* flash activity were analyzed using a LME model, with light pollution, predator, and the light pollution × predator interaction as fixed effects, and observation round (sunset, 1 hour after sunset, and 2 hours after sunset) and trial as random effects. Effects of light pollution on *P. versicolor* flash activity during the final two observation rounds (one hour after sunset and two hours after sunset) were analyzed using a generalized linear mixed effects (GLME) model, specifying a binomial distribution (female did or did not flash) and the logit link function. Light pollution was a fixed effect and observation round and trial were treated as random effects. *Photuris versicolor* flashes at sunset were excluded from the model as there was little to no flashing at this time. The number of *P. pyralis* flashes per minute was log transformed to improve the normality of the LME model residuals. Effects of light pollution and predator presence on whether or not the female *P. pyralis* mated were tested using a GLME model, specifying a binomial distribution and the logit link function, with light pollution and predator presence as fixed effects, and date as a random effect.

Firefly attraction to artificial lights

I conducted an additional experiment to test whether fireflies are attracted to or repulsed from, artificial light at night. I counted firefly individuals on paired lit and unlit sheet traps hung in lawn areas at BEF. Each sheet trap consisted of an opaque white plastic sheet (177 w × 182 cm) hung between two vertical objects (*e.g.,* trees, fenceposts, etc.) at a height of 1.5 m so that the bottom edge of the shower curtain just touched the ground. Traps were lit with an LED floodlight (Ultra-Tow 9-32 Volt LED Floodlight) positioned 0.3 m above the ground and 1.5 m away from the sheet, with the light pointed at the center of the sheet. The paired lit and unlit traps were located 10 m apart. I counted fireflies on the traps for 15 pairs of traps over the course of 14 nights at sunset, one hour after sunset, two hours after sunset, and midnight. I stopped the trials at midnight because firefly flashing activities at BEF are highest between sunset and midnight, and because insect capture using LED lights is typically higher before midnight than between midnight and dawn (Wakefield *et al.* 2016). Effects of light pollution on the numbers of *P. pyralis* and *P. versicolor* on the traps was analyzed using a LME model with light pollution as the fixed effect and observation round (sunset, 1 hour after sunset, 2 hours after sunset, or midnight) as both a fixed and random effect (Bondell *et al.* 2011). Observation round is included as both a fixed and a random effect because I was interested in changes in firefly captures throughout the evening, but observation round cannot be randomly assigned. The numbers of *P. pyralis* or *P. versicolor* captured on the traps were log transformed to improve the normality of the LME model residuals. All statistical analyses were conducted in R (R Core Team 2015). The LME and GLME models were performed using the R package ‘lme4’ (Bates *et al.*2015).

Results

Photuris versicolor courtship

Female *P. versicolor* tethered under artificial lights never flashed, whereas all 11 females tethered in unlit plots flashed at least once. On average, there were 7.27 ± 9.08 flashes from males within 1 m of each female in unlit plots, but males never flashed near females in lit plots. The difference in number of male flashes between lit and unlit plots was highly significant (t_{20} = 3.17, $p = 0.005$).

Predator-prey interactions and prey mating behaviors

In the predator-prey experiment, light pollution decreased male *P. pyralis* (prey species) flashes by 25% (Fig. 1a; $t_{5,485} = 2.93$, $p = 0.004$). There was no significant effect of the presence of a predator ($t_{5,485} = 0.410$, $p = 0.681$), and no significant interactive effect of predator presence and light pollution ($t_{5,485} = -1.57$, $p = 0.117$) on the number of male *P. pyralis* flashes. Light pollution significantly decreased the number of *P. versicolor* (predator species) flashes (Fig. 1b; $z = 5.56$, $p \leq 0.001$). None of the marked *P. pyralis* were eaten during this experiment, as all marked individuals were recovered alive. Twice as many female *P. pyralis* mated in lit cages compared to unlit cages (Fig. 2), however, this difference was not significant ($z = 1.58$, $p = 0.114$). The presence or absence of a predator had no significant effect on the portion of *P. pyralis* females that mated ($z = 0.453$, $p = 0.651$).

Firefly attraction to artificial lights

On average, 189% more *P. pyralis* were found on the lit sheet traps than the unlit sheet traps by the end of each collection night (i.e., midnight) (Fig. 3a; $t_{1,14} = -9.76$, $p \leq 0.001$). The lit traps captured, on average, 0.21 ± 0.52 *P. versicolor*, while no *P. versicolor* were found on the unlit traps (Fig. 3b; $t_{4,113} = -3.27$, $p = 0.001$). For both species, the number found on the traps varied significantly among rounds for both *P. pyralis* ($t_{1,14} = -4.23$, $p = 0.048$) and *P. versicolor* ($t_{1,14} = 2.15$, $p = 0.034$), with the number of individuals increasing over the course of the evening (Fig. 3).

Discussion

Gaston and Bennie (2014) proposed that light polluted areas may act as population sinks (immigration > emigration and mortality > births). However, few studies have assessed effects of light pollution on multiple demographic processes in any single species (Gaston and Bennie 2014, but see (Mclay *et al.* 2017, McMahon *et al.* 2017). In this study, I found that *P. pyralis* and *P. versicolor* fireflies were attracted to ‘white’ LED lighting (Fig. 3), which is rapidly becoming a dominant outdoor lighting technology (Baumgartner *et al.* 2012, Stanley *et al.* 2015). My results also show that ‘white’ LED lighting at night reduced the courtship behavior (flashing) and mating of *P. pyralis*, consistent with the findings of Firebaugh and Haynes (2016), while also strongly reducing flashing by *P. versicolor*. I not able to assess effects of light pollution on *P. versicolor* mating success, but the lack of *P. versicolor* flashing activity under light polluted conditions suggests mating would also be reduced in this species. For fireflies, the combined effects of nighttime LED lighting – attraction, strongly reduced flashing, and decreased mating success – suggests areas where outdoor LED lighting is installed may become demographic traps. The rapid accumulation of fireflies on sheet traps lit by LED lighting but not on unlit control sheet traps indicates this LED lighting caused immigration to exceed emigration. An important question for future research is whether the attraction of nocturnal insects to light polluted areas, coupled with decreases in courtship and mating, leads to the creation of population sinks.

I found no evidence for lethal or sub-lethal effects of *P. versicolor* presence on *P. pyralis*. *P. pyralis* were not eaten by *P. versicolor* during the mesocosm experiment, and *P. pyralis* flashing activity was the same in the presence or absence of *P. versicolor* (Fig. 1a). It is possible the mesocosms altered *P. versicolor* activity levels or flight behavior, but *P. versicolor* appeared to exhibit typical flying and flashing behaviors in the mesocosms. The lack of predation in the mesocosm experiment suggests predation of *P. pyralis* by *P. versicolor* rates may occur infrequently in field populations. This explanation seems plausible given that *Photuris* primarily consume *Photinus* to acquire defensive compounds (Eisner *et al.*1997); predation rates might be higher if *Photuris* consumed *Photinus* to meet nutritional needs.

Light pollution has the potential to intensify (Rydell 2006, Miller *et al.* 2017) or weaken (McMahon *et al.* 2017) intra-and inter-specific interactions through its effects on movement and behavior. Though my results suggest the predator-prey interactions between *P. versicolor* and *P. pyralis* is weak (*P. versicolor* never preyed upon *P. pyralis* in my mesocosm experiment), light pollution may further weaken this interaction because light pollution strongly inhibited flashing behaviors (Fig. 1b), which *Photuris* use to lure *Photinus.* Though I found that both species aggregate near artificial lights, which could intensify interactions by increasing encounters between individuals, it seems likely light pollution weakens both the intra-specific (mating) and inter-specific interactions (predation) of *P. versicolor* and *P. pyralis* given that these interactions are mediated by flashing dialogues.

Light pollution has long been recognized as a potential threat to nocturnal insect populations (Frank 1988), but causal links between light pollution and these declines have rarely been demonstrated (Fox 2013). Experimental evidence has shown that light pollution impacts a variety of demographic processes in nocturnal insects. For example, Botha *et al.* (2017) and van Geffen *et al.* (2015a) find light pollution alters mating probabilities in cricket and geometrid moths, respectively. Additionally, light pollution has been shown to increase mortality by elevating predation risk, such as for some moths predated by bats (Rydell 2006), and to incite behaviors leading to mortality, such as flying around lights to the point of exhaustion (Eisenbeis 2006, Shimoda and Honda 2013). However, because light pollution is correlated with other factors associated with urbanization such as changes in landcover type (*e.g.*, Doll 2008), demonstrably attributing observed declines in nocturnal insect populations to increased light pollution is precarious without the support of manipulative experiments, such as those presented here.

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Tables & Figures

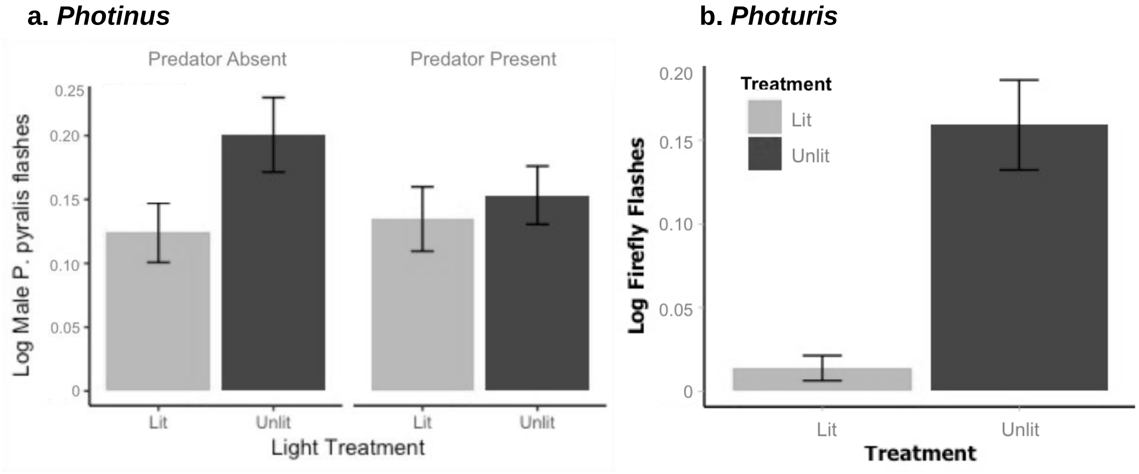

Figure 1. Number of *P. pyralis* (a) and *P. versicolor* (b) flashes in experimental mesocosms with and without artificial illumination.

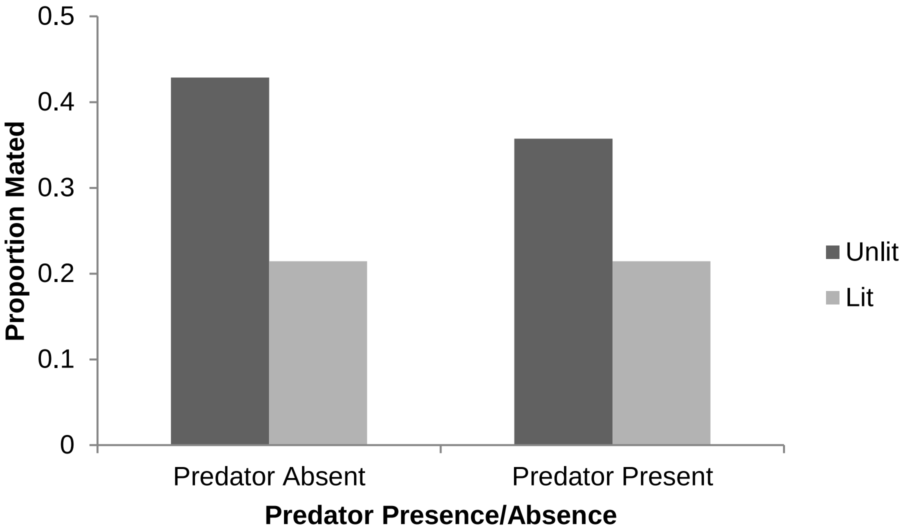

Figure 2. Proportion of *Photinus pyralis* females that mated in mesocosms that were or were not artificially lit, in the presence or absence of *Photuris versicolor* predators.

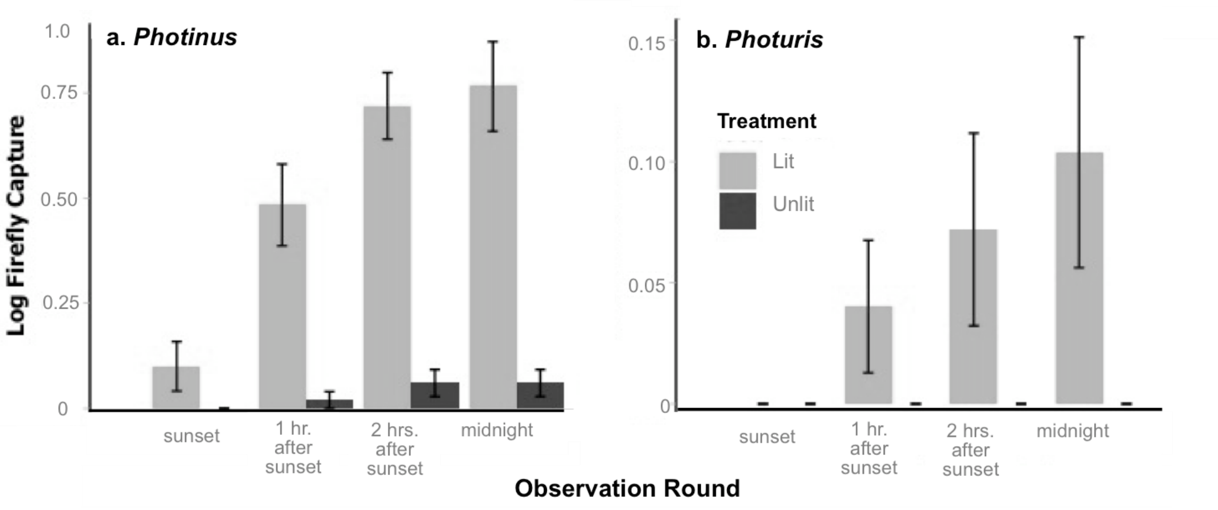

Figure 3. Number of *Photinus pyralis* (a.) and *Photuris versicolor* (b.) observed on lit and unlit sheet traps at sunset, 1 hour after sunset, 2 hours after sunset, and midnight.

Chapter 3

Evaluation of the efficacy of citizen science and multi-scale impacts of light pollution on fireflies

Abstract

Light pollution is a symptom of urbanization whose impact on species' abundances and distributions is poorly understood. Monitoring populations across the vast areas affected by light pollution is a task professional scientists may have difficulty accomplishing alone, but one solution—enlisting the aid of citizen scientists— is potentially under-utilized due to concerns about the quality of citizen science data. In this study, I examined the effects of light pollution and urbanization on firefly abundances and species richness using field survey data, citizen science data, and remote sensing data. This combination of datasets allowed me to assess the spatial scales at which light pollution/urbanization effects emerged. Analyses of scientist- and citizen scientist-collected data revealed similar factors as potential stressors for firefly populations. In almost all models, local (i.e., site-level) light pollution was negatively associated with firefly abundance and species richness. In citizen scientist-collected data, impervious surface within 0-2 km of the site and light pollution within 8-10 km of the site were also negatively associated with firefly abundance and species richness. The suite of findings emerging from these analyses— 1) that light pollution at multiple spatial scales was negatively associated with firefly abundance and richness, 2) that light pollution impacts were statistically distinguishable from impacts of urban land cover, and 3) that scientist and citizen scientist data reveal similar trends— describe both a problem and a solution. Fireflies appear to be facing a new stressor in the form of light pollution, and citizen scientists may have a key role to play monitoring light pollution impacts on firefly populations going forward.

Introduction

Earth's population will be predominately urban by 2030 (United Nations, Department of Economic and Social Affairs 2014). In the Unites States, moderate-density exurban areas are experiencing the fastest rate of growth (Katz *et al.* 2003). Land use change and the suite of associated perturbations are affecting increasingly large areas and increasing numbers of organisms.

Light pollution— artificial light at night—increases concurrently with urbanization (Sutton 2003). By some estimates, light pollution covers 23% of the terrestrial surface of the Earth between 75°N and 60°S (Falchi *et al.* 2016b), and is growing spatially at a rate of 2.2% per year (Kyba *et al.* 2017). A growing body of literature suggests light pollution may have wide-ranging effects on organisms' physiology, behavior, reproduction, and mortality (reviewed in Gaston *et al.* 2013). A number of studies examine organisms' responses to light pollution in a lab or locally around a small number of streetlights (Stone *et al.* 2012, Perkin *et al.* 2014). Few studies examine light pollution effects across large areas, and impacts of light pollution on populations are largely unknown (Kyba and Hölker 2013, but see Langevelde *et al.* 2018). Linking organismal impacts to impacts on populations and communities will be a critical challenge in the field going forward (Gaston *et al.* 2014, Stanley *et al.* 2015)

Here, I sought to understand how land use (degree of urbanization) and light pollution affect abundance and species richness of group of nocturnal insects—fireflies (Coleoptera: Lampyridae). I combined field surveys and geospatial analysis of remote sensing data to examine the spatial scales over which light pollution and urbanization affects emerged. I also contrast my data with data from a citizen science project with the goal of broadly assessing the comparability of these data.

Citizen science plays an increasingly critical role in monitoring species' distributions, phenologies, and abundances. Schmeller *et al.* (2008) estimated that citizen scientists in Europe make up 86% of participants in biological monitoring programs, with an associated annual savings of 4 million Euros. By recruiting volunteers to collect data, these programs allow scientists to increase sampling effort at minimal cost. Many studies report similar patterns in data collected by citizen and professional scientists. For example, Kremen *et al.* (2011) and Delaney *et al.* (2008) showed scientists and citizen scientists count similar numbers of species in arthropod surveys. However, concerns that data collected by non-experts are less accurate than data collected by professional scientists potentially limit the use of citizen science data in the primary literature (reviewed in Burgess *et al.* 2017), especially since many citizen science programs lack a rigorous system for evaluating data quality (Lewandowski and Specht 2015).

In this study, I compared data collected by a professional scientist (i.e., me) with data emerging from a citizen science program (Firefly Watch) to discern whether these datasets surfaced similar or dissimilar factors associated with firefly abundance and species richness.[*] I quantified light pollution and urban land cover at the site level and in the surrounding landscape within 0-2 km and 8-10 km of the site (i.e., landscape context). I took an additional step to partition the impacts of light pollution and urban land cover. I reduced collinearity between these

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[*] Note: I use the term "species richness" throughout this chapter to refer to the number of species observed at a site. In the scientist-collected dataset, species richness is truly a count of the number of species recorded. In the citizen scientist-collected data, species richness describes the number of firefly flash patterns reported at a site. For simplicity, I use "species richness" to refer to both measures.

two entangled variables by sampling fireflies at locations where light pollution was lower or higher than was typical given the amount of impervious surface in surrounding areas.

Because light pollution and other changes associated with urbanization (e.g., impervious surface) increase hand-in-hand, one factor is sometimes used as a proxy for the other in ecological studies (Bennie *et al.* 2014). Equivalating light pollution and urban land cover assumes organisms respond similarly to both anthropogenic disturbances, at least at some spatial scales. However, evidence from small-scale studies already undermines this assumption for some organisms. Light pollution independent of land cover has been shown to influence foraging behavior (Rydell 1991, Minnaar *et al.* 2015, Hale *et al.* 2015), mating behavior (van Geffen *et al.* 2015a, Firebaugh and Haynes 2016), and abundance (Firebaugh and Haynes 2016). Unless an attempt is made to separate the effects of light pollution from urban land cover in ecological studies, it will be difficult to make informed management decisions to mitigate light pollution impacts on organisms.

Assessing light pollution and urbanization within different distances of study sites yielded insight into the importance of landscape context in this system. Landscape context has been shown to impact arthropod abundances and diversity within fragmented landscapes. For example, McFrederick *et al.* (2008) found the proportion of natural land cover surrounding urban parks was positively associated with bumblebee abundance in the parks, and Steffan-Dewenter *et al.* (2002) found the proportion of semi-natural habitat in the surrounding landscape was positively associated with Hymenoptera species richness. The importance of landscape context may vary with spatial scale and within closely-related taxonomic groups. Steffan-Dewenter *et al.* (2002) found species richness of solitary wild bees was positively associated with the percentage of semi-natural habitat within 1 km, while bumblebee species richness was not associated with the percentage of semi-natural habitat within any of the distance classes examined (250 m-1 km). While landscape context traditionally describes land cover, this concept could also potentially describe light pollution in areas surrounding focal locations. To my knowledge, only one study has examined the spatial scales over which light pollution affects abundance. Azam *et al.* (2016) showed light pollution was negatively associated with abundances of three out of four insectivorous bat species in France at scales of 200 m – 1 km. The amount of light pollution in areas surrounding focal sites is conceivably important for fireflies because light pollution could impact rates of reproduction locally (Firebaugh and Haynes 2016) as well as immigration from populations in surrounding areas.

I predicted scientist and citizen scientist-collected data would reveal similar relationships among firefly abundances, species richness, light pollution, and urban land cover. This prediction was informed by previous studies reporting similar trends in scientist-collected and citizen-scientist-collected data, such as accuracy of species identification (Delaney *et al.* 2008), species richness and abundance (Kremen *et al.* 2011), and spatial patterns of species' distributions (Lin *et al.* 2015). Based on the spatial scales at which urbanization impacts abundances of other insects (Meineke *et al.* 2013, Bennett *et al.* 2013, Penone *et al.* 2013, Concepción *et al.* 2015), I predicted light pollution and impervious surface would be negatively associated with firefly abundance and species richness at local (i.e., site-level) and intermediate (within 0-2 km of the site) spatial scales, but there would be no association at large spatial scales (within 8-10 km of the site).

Methods

Study system

There are 120 described firefly species in North America (Lloyd 2004). The adults of many firefly species produce bioluminescent flashes. These flashes allow males and females to identify and communicate with conspecific mates during courtship prior to mating (Lloyd 1971). Due to the unique, flash-based communication system used in courtship, fireflies are ideal for studying light pollution effects on behavior. Firefly flashing activities are sensitive to environmental light conditions. Flashing begins at or sometime after sunset when ambient light levels are low (Lall *et al.* 1980), and the timing of nightly flashing activities can be advanced or delayed by natural variation in light levels due to cloud cover or the phase of the moon (Allard 1931, Dreisig 1975). The importance of light as a cue for firefly flashing has been corroborated by laboratory behavioral studies, which show that exposure to artificial light can stop or delay the timing of firefly flashing (Rau 1932, Buck 1937, Dreisig 1975, Merritt *et al.* 2012).

In this study, I paid particular attention to two taxonomic groups of fireflies abundant in the eastern United States (Faust 2017). The first, *Photinus pyralis*, is a widely-distributed species that begins flashing around sunset. The second, fireflies in the genus *Photuris*, begin flashing sometime after sunset. Previously, I showed light pollution decreases abundances, disrupts courtship flashing and attracts *P. pyralis* and *Photuris versicolor* fireflies (Firebaugh and Haynes 2016; Chapter 2). These results suggest light pollution may create demographic traps, luring fireflies into areas where they may be less likely to mate, and giving rise to areas where rates of immigration and death exceed rates of emigration and birth. Here, I explored whether large-scale spatial patterns in abundance were consistent with the hypothesis that light pollution creates demographic traps for fireflies.

Survey of fireflies in Virginia

In summer 2017, I surveyed firefly abundances and species richness at 45 residential properties in Virginia. These properties were located in or near five municipalities (towns or cities; Winchester, Leesburg, Charlottesville, Richmond, and Roanoke), with nine properties surveyed per municipality. I contacted property owners through social and professional contacts, and through the Virginia Master Naturalists Program, a state-wide naturalist organization. To reduce the correlation between urban land cover and light pollution within the set of available study sites (properties), which could inflate collinearity in models predicting firefly abundances or species richness, I deliberately selected properties that were brighter or darker than expected based on the amount of nearby impervious surface. I calculated mean illuminance (VIRRS 2012; Elvidge *et al.* 2017)) and proportion of impervious surface (NLCD 2011; Homer *et al.* 2015) within 1 km of each property in ArcGIS (ESRI Press, Redlands, CA), regressed illuminance against the proportion of impervious surface, and iteratively removed properties close to the fitted regression line until I was left with a subset of 9 properties for each municipality with the lowest possible R^2 value. In all, 62 properties were excluded from the survey using this method.

I surveyed all properties within each municipality consecutively, as it would have been impractical to travel from municipality to municipality each day. At each residential property, I marked out a 10 ×10 m plot located 2-5 m from the house, or a built element associated with the house such as a deck. Occasionally, the plot was smaller than 10 ×10 m to accommodate small or irregularly-shaped yards. The plot was laid in the front, back, or side yard based on the homeowners’ preference. Plot boundaries were marked with orange landscape flags and with blue, battery-operated LED tealights (Samyo, powered by 3V Lithium battery, 3 × 3 × 2.54 cm) to facilitate nighttime plot delineation. These lights were chosen because fireflies are thought to be unable to see blue light (Lall and Worthy 2000).

At sunset, 30 minutes after sunset, and 1 hour after sunset, I determined the mean number of firefly flashes per species within each plot. Counts of firefly flashes during peak activity are a reasonable proxy for abundances (Firebaugh and Haynes 2016). The means were calculated from 3 1-minute counts taken from different sides of the plot. Counts were taken from different sides of the plot in case some flashes were obstructed by objects in the plot such as trees or bushes. I identified species based on their flash patterns.

After the final observation round, I divided the plot interior into 2 × 2 m grids and recorded the dominant land cover class (lawn, forb, bush, tree canopy) and illuminance (lux) for each grid cell. Light pollution within each plot was estimated as the mean of the illuminance measures across grid cells from 2-8 m (0 and 10 m grid points at the plot periphery were excluded). Illuminance was measured using a handheld lux meter (ExTech LT300) at chest height with the sensor pointed directly upward. Mean light pollution and proportion of impervious land cover were calculated from satellite imagery 0-2 km and 8-10 km of each site using ArcGIS 10.4 (ESRI; Redlands, CA). I chose widely separated annuli to reduce the potential for collinearity.

The relationships between firefly abundance (i.e., number of flashes), firefly species richness, land cover, and illuminance at multiple spatial scales were analyzed using linear mixed-effects models. Because samples of higher numbers of individuals are more likely to include higher numbers of species, I used the Chao I estimator of species richness (Chao 1984) to correct for effects of sample size on species richness. I included municipality as a random effect to account for the spatial and temporal proximity of measures taken within each municipality. Fixed effects included light pollution within 0-2 and 8-10 km of the property (VIIRS 2012; Elvidge *et al.* 2017), impervious surface within 0-2 km and 8-10 km of the property (NLCD 2011; Homer *et al.* 2015), the proportion of the plot that was lawn, the proportion of the plot with overhanging tree canopy, and illuminance within the plot. To avoid multicollinearity among fixed effects, I removed variables with variance inflation factors above 10 (Montgomery and Peck 1992).

Analysis of citizen science data

I compared data from my firefly survey with data from Firefly Watch, a national citizen science program affiliated with the Boston Museum of Science. Firefly Watch participants monitor firefly activities in a survey location of their choice throughout the window of adult firefly activity (usually May-August), along with ecological and physical characteristics of the site including habitat type (lawn, forest, wetland, etc.) and whether there is light pollution present.

I estimated firefly abundance from Firefly Watch question 9 (“During a 10-second period, how many fireflies did you see?”). For this question, Firefly Watch participants record the total number of firefly flashes observed in 10 seconds at their chosen survey location as a categorical variable (*e.g.*, None, 1, 2-5, etc.). I estimated firefly species richness from Firefly Watch question 7 (“How many different firefly flashing patterns did you observe?”). Many firefly species have characteristic flash patterns (Lloyd 1966), so the number of flash patterns observed should give some indication of the number of species present.

Firefly Watch participants also provide an assessment of light pollution at the site. They report whether artificial lights at the site are: 1) never on, 2) on sporadically (i.e., activated by a motion sensor), 3) on for a portion of the night (“>1 hour, not all night”), or 4) always on. To create a more ordered, hierarchical structure in these reported light pollution categories (i.e., no light pollution, moderate light pollution, severe light pollution), I collapsed the four light pollution categories into three categories for the analysis: lights are 1) never on, 2) sometimes on (motion sensor, on for less than one hour each night), or 3) always on.

Because Firefly Watch participants choose how frequently or infrequently they make observations, some sites appear in the data more frequently than others. To achieve equal representation of sites, I collapsed all observations for each site into a single record describing either abundance or species richness. For example, a site reporting 5 instances of 2-5 flashes per 10 seconds and 2 instances of 0 fireflies would be represented as one record of 2-5 flashes per 10 seconds. Thus, the response variables used in the analyses can be thought of as the “modes” of abundance or species richness per site.

The relationships among firefly abundance, impervious surface, and light pollution at each site and in the surrounding landscape (i.e., landscape context) were analyzed using a cumulative link model. An ordinal regression approach is necessary because Firefly Watch participants record firefly abundance as a categorical variable (e.g., 0 flashes seen in 10 seconds, 1 flash, 2-5 flashes, etc.). To account for spatial autocorrelation, I included an autocovariate in the models consisting of the weighted average of the response variable at neighboring locations (Augustin *et al.* 1996), with each weight equal to the inverse of the distance to the neighboring location. The fixed effects in the model were light pollution within 0-2 and 8-10 km of the site, impervious surface within 0-2 and 8-10 km of the site, the presence of lawn at the site, and the presence of light pollution at the site (*i.e.*, outdoor lights on the property are turned on all the time, some of the time, or never). Due to the lack of collinearity metrics for ordinal regressions, I resorted to using the correlation coefficient to assess relationships among explanatory variables pre-analyses. Following Elith *et al.* (2006), variables were removed from a model until no pairwise correlations (r) between explanatory variables were > 0.85.

For all statistical analyses, I used multi-model inference procedures to rank candidate models based on parsimony (Burnham and Anderson 2002). Following Burham and Anderson (2002), models with ΔAICc < 2 were deemed to have substantial support.

All statistical analyses were conducted in R (R Core Team 2015). For the scientist-collected data, linear mixed-effects models were performed using the package 'lme4' (Bates *et al.* 2015). *Photinus pyralis* abundance at sunset and Chao I species richness were log transformed to meet test assumptions. For the citizen scientist-collected data, cumulative link models were performed using the package 'MuMIn' (Bartoń 2016). The autocovariate term accounting for spatial autocorrelation was constructed using package 'spdep' (Bivand and Piras 2015). Automated model selection was performed using the 'dredge' function in package 'MuMIn' (Bartoń 2016).

Results

Survey of fireflies in Virginia

Fireflies were present in 97.77% of the plots. *Photinus pyralis* activity was highest at sunset, while *Photuris* activity peaked one hour after sunset (Table 1). Average species richness was 3.05 ± 0.97 (Table 2). *Photinus pyralis* was observed at every site where fireflies were present. Fireflies in the genus *Photuris* were observed in 71.11% of the plots.

Problems identified during preliminary analyses indicated that models could not be run as originally conceived. Based on inspection of variance inflation factors, light pollution within 0-2 km of the site was excluded from the final models (VIF = 11.18). Additionally, because counts of firefly flashes were almost always zero during non-peak times (sunset for *P. pyralis* and 30 minutes after sunset for *Photuris*), I decided to only analyze peak abundance for each group of fireflies. Finally, in the analysis of species richness data, a model containing the intercept and no other explanatory variables was included among models receiving “substantial support” (e.g., Δ AICc less than 2; Burnham and Anderson 2002). Because I had little confidence the highest ranking models would be useful for prediction, I do not report results from the analysis of species richness for the scientist-collected dataset.

Out of 64 candidate models describing *P. pyralis* abundance at sunset, 8 models received substantial support (ΔAICc < 2; Table 3). Distinguishing among these 8 models was difficult because they differed only slightly in their AICc weights, i.e., the probability of being the highest ranked model. The proportion of the plot covered in tree canopy appeared in almost all of the models receiving substantial support, and the proportion of the plot covered in lawn appeared in half of these models. Light pollution within 8-10 km of the site appeared in 3 of 8 the supported models. Other explanatory variables appeared infrequently. Light pollution at the site appeared in none of the models receiving substantial support.

Out of 64 candidate models describing *Photuris* abundance 30 minutes after sunset, 5 models received substantial support (ΔAICc < 2; Table 4). Two models were weighted considerably higher than the others. In these two models, light pollution at the site was negatively associated with abundance, and impervious surface was positively associated with abundance. The model receiving the second highest weight also contained the proportion of the plot covered in tree canopy. Light pollution at the site appeared in all models receiving substantial support, and the relationship between light pollution at the site and *Photuris* abundance was always negative. Impervious surface within 0-2 km of the site was positively associated with abundance in 4 out of 5 models receiving substantial support. Other variables appearing in models receiving substantial support included canopy cover and lawn.

Analysis of data from a citizen science project

Most Firefly Watch participants reported high firefly abundances, with counts of 6-20+ flashes in 10 second observation periods representing the majority (75.62%) of observations (Figure 1). Firefly absence—observations of 0 firefly flashes in 10 seconds—was reported by 14.08% of participants. Mean species richness was similar—around 2-3 species per site— in scientist and citizen scientist-collected data (Table 2).

As with the scientist-collected data, preliminary analyses revealed light pollution within 0-2 km to be highly correlated with light pollution within 8-10 km (r = 0.89). I decided to remove light pollution within 0-2 km instead of 8-10 km because this allowed me to assess light pollution within the same distance classes in the analyses of scientist and citizen scientist data.

Two of the 64 candidate models predicting firefly abundance received substantial support (ΔAICc < 2; Table 5). The weight of the most parsimonious model was almost double that of the second most-parsimonious model. (Table 5). Both models contained light pollution at the site, impervious surface within 0-2 km, impervious surface within 8-10 km, and light pollution within 8-10 km. Impervious surface within 8-10 km of the site was positively associated with firefly abundance, while impervious surface within 0-2 km and impervious surface within 8-10 km were negatively associated with firefly abundance. Lower firefly abundances were reported at sites with more severe light pollution (Figure 3). The second-highest ranked model contained all of the variables in the highest-ranked model with the addition of the presence or absence of lawn at the site. Lower firefly abundances were reported at sites where lawn was present.

Out of 128 candidate models predicting species richness observed by citizen scientists, 2 models received substantial support (ΔAICc < 2; Table 6). The weight of the highest-ranked model was nearly double that of the second highest-ranked model. Impervious surface within 0-2 and 8-10 km of the site and light pollution within 8-10 km of the site were all negatively associated with firefly species richness in both models. Light pollution at the site also appeared in both models. Higher numbers of species were reported at sites with less severe light pollution (Figure 4). The second-highest ranked model contained all of the variables in the highest-ranked model, with the addition of the presence or absence of lawn. More firefly species were observed at locations where lawn was present.

Discussion

In this study, light pollution impacts on firefly abundances and species richness were statistically distinguishable from impacts of urban land cover. Light pollution measured over multiple spatial scales appeared in highly-ranked models predicting abundance (except those for *P. pyralis* abundance) and species richness, a finding underscoring both the importance of light pollution and the complexities associated with its control. Conserving fireflies in urbanizing landscapes may require collaboration among multiple stakeholders to reduce nighttime illumination within residential properties, neighborhoods, and municipalities.

Different combinations of factors influenced abundances of different types of fireflies in scientist-collected data. Site-level light pollution was negatively associated with abundances of fireflies in the genus *Photuris.* In contrast, land cover characteristics such as lawn and tree canopy cover were strongly associated with *Photinus pyralis* abundance. The importance of site-level light pollution for *Photuris* but not *P. pyralis* is consistent with manipulative field experiments showing light pollution caused larger reductions in *P. versicolor* abundance than *P. pyralis* abundance (Firebaugh and Haynes 2016, Ch. 2). *Photinus pyralis* may be less sensitive to light pollution than *Photuris* species because *P. pyralis* completes most of its flashing activities within an hour of sunset, when ambient light is brighter than artificial lighting. Varying effects of light pollution for species with different diel activity patterns has also been shown for other animals, such as bats (Azam *et al.* 2015) and moths (Langevelde *et al.* 2018). Together, these findings suggest that diel activity patterns may be a key trait for predicting which species will be most strongly impacted by light pollution, with nocturnal species more likely to be affected than diurnal or crepuscular species.

Surprising, firefly abundance was positively associated with impervious surface in a number of models (Tables 3-5). While some insect species, so-called “urban exploiters” (Kark *et al.* 2007) increase in abundance in urban areas (e.g., cockroaches, bedbugs), it is difficult to imagine why fireflies should belong to this group. Possibly, fireflies were responding to an unmeasured factor associated with impervious surface. It is also possible that habitat loss due to urbanization causes surviving individuals to aggregate into remaining patches of suitable habitat. A similar phenomenon known as “crowding” has been observed for some species experiencing habitat loss (Ewers and Didham 2006, Nielsen *et al.* 2014). The locations where citizen scientists and I chose to conduct firefly surveys were typically not heavily developed (100% percent of sites contained one or more semi-natural, non-lawn vegetation types). The urban and suburban yards constituting the majority of survey sites may have shown high firefly densities relative to intensively urbanized areas nearby.

To date, most work examining urbanization effects on beetles concerns ground-dwelling carabid beetles because carabids are abundant, diverse, and easy to sample using pitfall traps (Martinson and Raupp 2013). Carabid beetle abundance and species richness generally decrease with increasing urbanization (reviewed in Niemela and Kotze 2009, Martinson and Raupp 2013). Urbanization is also associated with decreases in abundance and species richness for two other groups of ground-dwelling beetles: dung beetles (Korasaki *et al.* 2013) and rove beetles (Magura 2013). However, Egerer *et al.* (2017) found ladybug abundance and species richness was higher in gardens surrounded by higher proportions of urban land cover. One potential explanation for varying effects of urbanization on species' abundances is that beetles with flying adults such as ladybugs and fireflies may be more able to cope with urbanization by dispersing among patches of semi-natural habitat embedded within urban landscapes.

In addition to investigating how light pollution and urban land cover may be impacting firefly populations, a second goal of the study was to compare scientist- and citizen scientist-collected data. I found a number of parallels. Mean species richness observed within sites was similar in my survey data and citizen science data. This result is consistent with other findings showing professional and citizen scientists produce similar species richness estimates in arthropod surveys (Kremen *et al.* 2011, and Delaney *et al.* 2008). Scientist- and citizen scientist-collected data also surfaced consonant factors as predictors of firefly abundance. In most supported models (except those for *P. pyralis* abundance), light pollution at the site was negatively associated with firefly abundance. Impervious surface within 0-2 km of the site also appeared in a number of the supported models for the two datasets. Large areas of agreement between scientist- and citizen scientist collected data suggest citizen science programs such as Firefly Watch may yield valuable monitoring data supporting firefly conservation in years to come.

A few differences also emerged from the comparison of scientist- and citizen scientist-collected data. While average species richness was similar for the two datasets overall, citizen scientists in Virginia reported multiple species less frequently than I did in study plots across Virginia. Firefly Watch participants in Virginia reported a single species in 52.8% of observations compared with 29.54% of observations in scientist-collected data (Table 2). There were also a few noteworthy differences regarding factors associated with firefly abundance. Impervious surface within 0-2 km of the site was positively associated with firefly abundance in my surveys, but was negatively associated with abundance as measured by citizen scientists. Additionally, impervious surface within 8-10 km of the site was positively associated with firefly abundance in citizen science-collected data, but was negatively associated with firefly abundance in scientist-collected data. I do not have a compelling explanation as to why impervious surface is negatively associated with abundance in one dataset but positively associated with abundance in another.

Multi-model selection was more successful at identifying, with high confidence, the most parsimonious models predicting firefly abundance in citizen scientist-collected data than in scientist-collected data. The large difference in AICc weights, which give the probability a given model is the most parsimonious model, may be a result of the much larger sample size for the citizen science dataset. In the Firefly Watch data, fireflies were observed in an average of 3,160 sites annually, compared to the 45 sites I was able to survey in one summer. The ability of citizen scientist programs to amass large numbers of observations across large areas renders these programs potentially valuable for monitoring firefly populations, and greatly expands the areas over which fireflies can be regularly surveyed.

Citizen science projects such as Firefly Watch must balance scientific and outreach objectives. Stricter protocols may facilitate collection of higher quality data, improving the utility of the data for scientific research. However, increasing methodological rigor (e.g., requiring citizen scientists to collect data on a weekly basis) may discourage participation. Depending on the goals of a particular citizen science program, adoption of stricter protocols may actually undermine the success of the program if decreased participation is the result.

I offer a number of suggestions that may enhance the scientific utility of Firefly Watch data, with the caveat that these suggestions should be weighed against other objectives of the program. First, I providing additional training on firefly species identification may increase reporting of multiple species. Using video webinars to show participants the flash patterns of different species might be one way to accomplish this. Second, clearer guidelines on how frequently data should be collected may increase the effective size of the dataset. Firefly Watch participants are encouraged to collect data once a week, but in practice, most participants collect data sporadically throughout the summer. Large differences in sampling effort across sites (1-139 observations per year) are statistically problematic. My choice to use only one observation per site corrected for differences in sampling effort across sites in the analysis, but also decreased the effective sample size ten-fold, an outcome that is hardly ideal. Small adjustments to the Firefly Watch program, such as providing additional training and setting a fixed data collection schedule with specified dates and times for data collection, might increase the scientific utility of this already large and valuable dataset.

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Tables & Figures

Table 1. Firefly abundances, as measured by counts of flashes, in a survey of fireflies on residential properties in Virginia conducted by a professional scientist.

Abundance (count of flashes)	Mean	St. Dev.	Min	Max
Total flashes	57.95	59.70	0	263
Sunset				
Photinus pyralis	10.27	13.64	0	63
Photuris	0	0	0	0
30 minutes after sunset				
Photinus pyralis	3.41	5.44	0	24
Photuris	0.64	1.28	0	6
60 minutes after sunset				
Photinus pyralis	0.27	0.52	0	3
Photuris	3.13	5.81	0	27

Table 2. Comparison of firefly species richness in scientist-collected data (species richness) and citizen-scientist-collected data (FFW; number of species observed) for all US sites and the subset of sites in Virginia. Estimates of species richness accounting for number of individuals observed (e.g., Chao I species richness estimates) are not displayed for Firefly Watch data because there could not be calculated because these metrics require numerical counts of abundances, but Firefly Watch participants report abundance as a categorical variable.

	% of Observations		
Species Richness	Scientist (VA)	FFW (all US)	FFW (VA sites)
0	2.27	6.59	10.00
1	29.55	51.26	52.80
2	36.36	26.97	18.09
3	27.27	7.75	6.98
> 3	4.55	7.42	12.12
Mean Species Richness	3.05 ± 0.97	2.58 ± 1.05	2.56 ± 1.08

Table 3. Rankings of linear mixed-effects models describing *Photinus pyralis* abundance at sunset in scientist-collected data. Multi-model inference procedures were used to rank 64 candidate models based on parsimony. Models with ΔAICc < 2 were deemed to have substantial support, and models with ΔAICc > 2 are not shown.

Intercept	**Site Light**	**Canopy**	**Lawn**	**Imperv 0-2 km**	**Imperv 8-10 km**	**Light 8-10 km**	**ΔAICc**	**AICc weight**	**R^2**
-2.22		3.98					0	0.07	0.11
0.25		2.96	-3.01				0.06	0.07	0.16
2.24			-4.13				0.15	0.07	0.11
-3.71		4.21				0.06	0.26	0.07	0.16
-3.14		4.71		0.08			0.30	0.06	0.16
-0.79		3.69	-2.74	0.07			0.84	0.05	0.20
-4.26		3.91			-0.17	0.13	1.57	0.03	0.19
-1.36		3.41	-2.35			0.04	1.67	0.03	0.18

Table 4. Rankings of linear mixed-effects models describing *Photuris* abundance 30 minutes in scientist-collected data. Multi-model inference procedures were used to rank 64 candidate models based on parsimony. Models with ΔAICc < 2 were deemed to have substantial support, and models with ΔAICc > 2 are not shown.

Intercept	**Canopy**	**Lawn**	**Site Light**	**Imperv 0-2 km**	**Imperv 8-10 km**	**Light 8-10 km**	**ΔAICc**	**AICc weight**	**R^2**
0.65			-6.64	0.05			0	0.24	0.24
0.31	0.62		-5.96	0.05			0.75	0.17	0.27
0.81			-2.95				1.56	0.11	0.01
0.52		0.25	-7.43	0.05			1.84	0.10	0.24
-0.07	0.80	0.56	-7.48	0.06			1.94	0.09	0.28

Figure 1. Firefly abundances, as measured by counts of flashes, in citizen scientist-collected data emerging from Firefly Watch. These data show the abundance category (0 flashes, 1 flash, 2-5 flashes, etc.) most commonly reported at each Firefly Watch site.

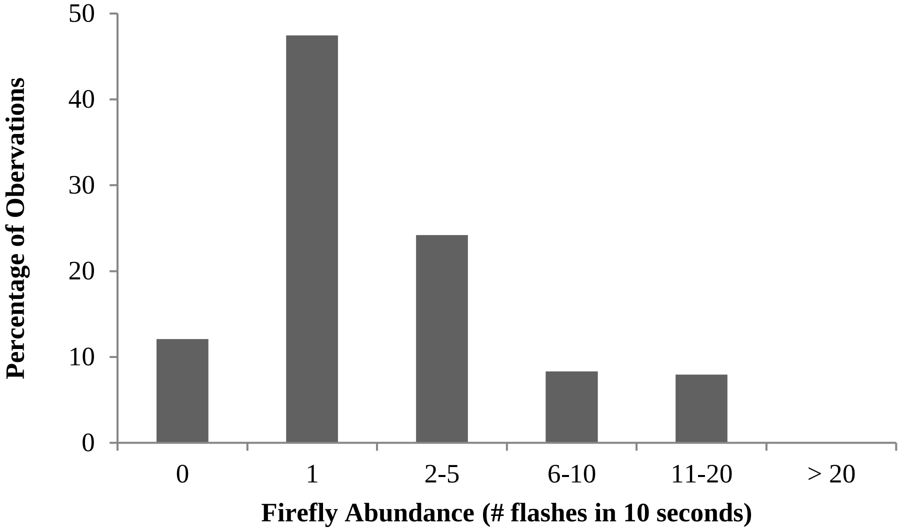


Figure 2. Comparison of firefly species richness in scientist-collected data (VA) and citizen-scientist-collected data (Firefly Watch = FFW) for all US sites and the subset of sites in Virginia. Estimates of species richness accounting for number of individuals observed (e.g., Chao I species richness estimates) are not displayed because there could not be calculated because these metrics require numerical counts of abundances, but Firefly Watch participants report abundance as a categorical variable.

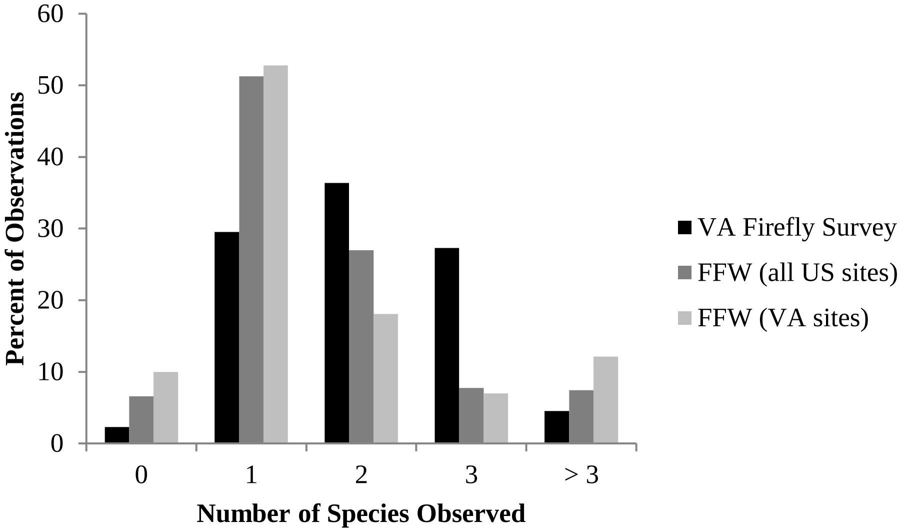


Table 5. Parsimonious cumulative link models describing firefly abundance from Firefly Watch citizen science data. Multi-model inference procedures were used to rank 64 candidate models based on parsimony. Models with ΔAICc < 2 were deemed to have substantial support, and models with ΔAICc > 2 are not shown. The symbol "•" indicates that a given categorical variable was included in the model.

Intercept	**Spatially-Lagged Variable**	**Lawn**	**Site Light**	**Imperv 0-2 km**	**Imperv 8-10 km**	**Light 8-10 km**	**ΔAICc**	**AICc weight**
•	< 0.001		•	-0.02	0.01	-0.01	0	0.66
•	< 0.001	•	•	-0.02	0.01	-0.01	1.30	0.34

Figure 3. Associations between light pollution categories and the firefly abundance categories at the sites surveyed by citizen scientists. Firefly Watch citizen scientists report whether artificial lights at the site are never on, sometimes on, or on all of the time.

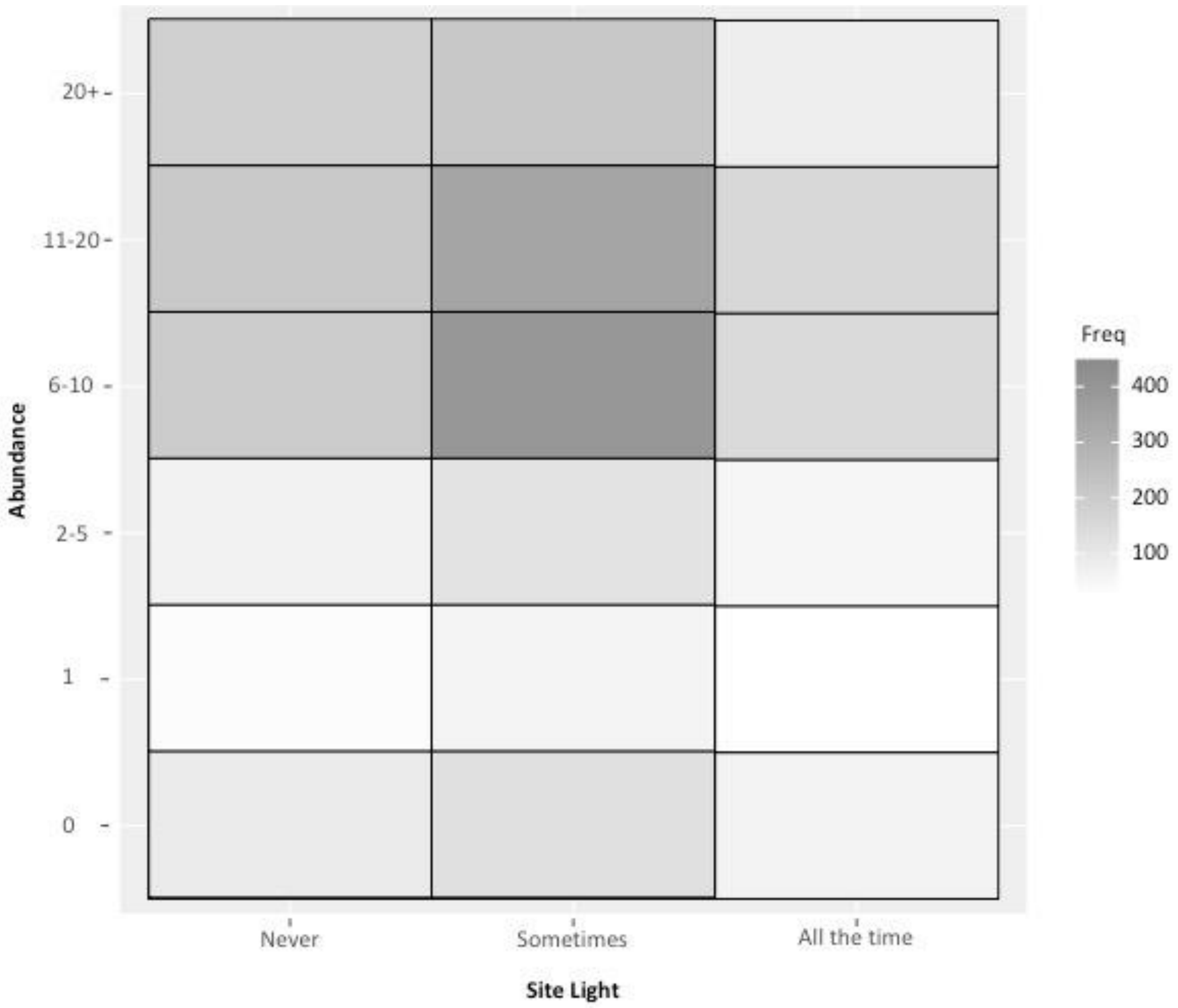
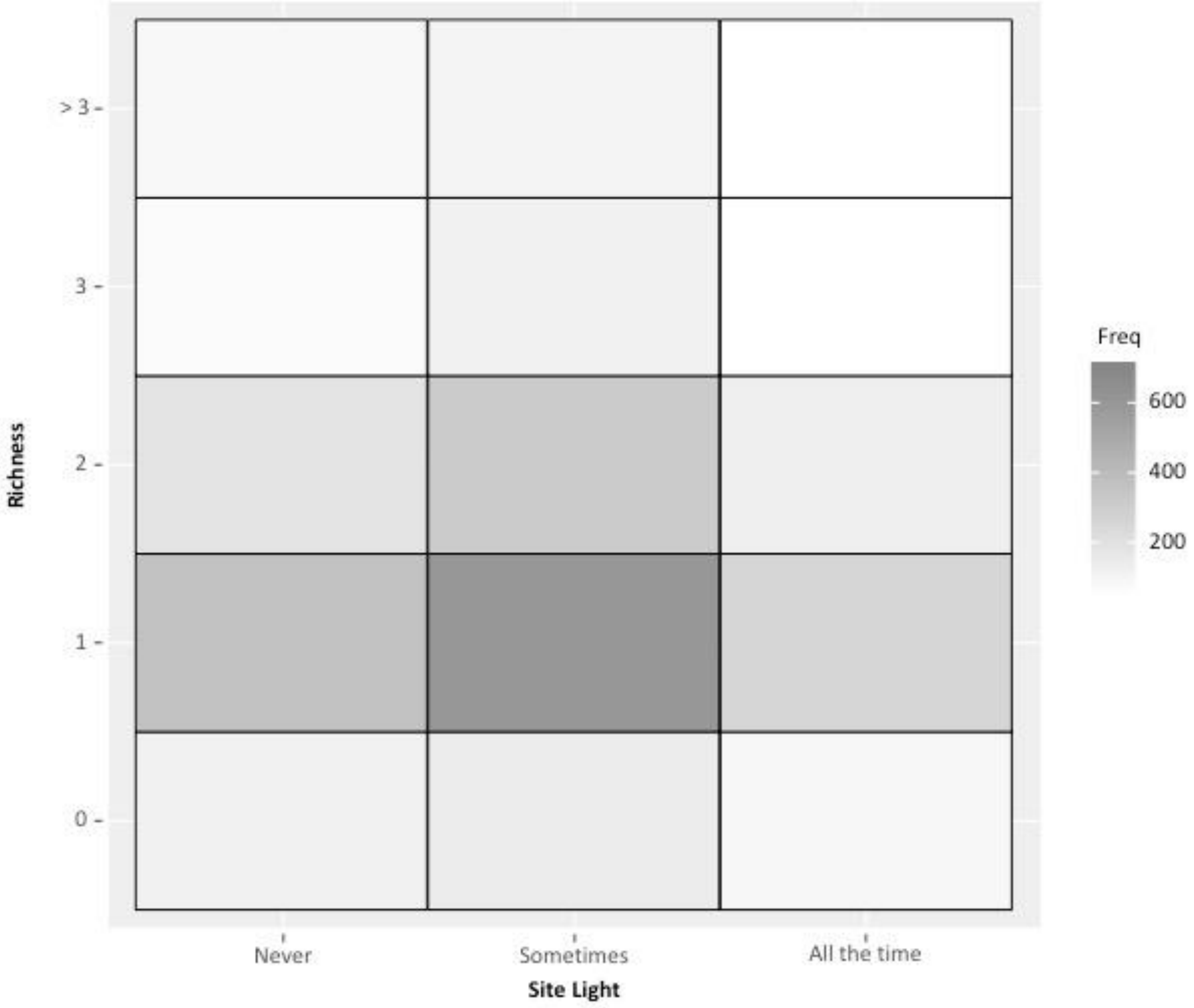


Table 6. Parsimonious cumulative link models describing the number of firefly species observed by the citizen scientists. Multi-model inference procedures were used to rank 128 candidate models based on parsimony. Models with ΔAICc < 2 were deemed to have substantial support, and models with ΔAICc > 2 are not shown. The symbol "•" indicates that a given categorical variable was included in the model.

Intercept	**Spatially-Lagged Variable**	**Lawn**	**Site Light**	**Imperv 0-2 km**	**Imperv 8-10 km**	**Light 8-10 km**	**Abundance**	**ΔAICc**	**AICc weight**
•	< 0.001		•	-0.01	-0.01	< -0.001	•	0.00	0.61
•	< 0.001	•	•	-0.01	-0.01	< -0.001	•	1.60	0.28

Figure 4. Association between the light pollution categories and species richness observed categories observed by the citizen scientists. Firefly Watch citizen scientists report whether artificial lights at the site are never on, sometimes on, or on all of the time. Estimates of species richness accounting for number of individuals observed (e.g., Chao I species richness estimates) are not displayed because there could not be calculated because these metrics require numerical counts of abundances, but Firefly Watch participants report abundance as a categorical variable.



Chapter 4

Multi-year experiment shows no impact of light pollution on trophic structure of grassland arthropods

Abstract

The relative abundances of herbivores, predators, detritovores, and other trophic groups in a community (*trophic structure*) are commonly measured when examining light pollution impacts on communities, and may yield insights into how energy and nutrients flow through ecosystems. However, past studies often occur over short time scales unlikely to reflect the periods over which communities experience light pollution in the field. To examine longer-term impacts of light pollution on trophic structure, I experimentally manipulated light pollution in a grassland ecosystem and monitored arthropod communities in lit and unlit plots over two years. Arthropod abundances were higher in lit plots than in unlit plots during the first year of the study, but not in the second year of the study. Arthropod abundances within trophic groups did not differ in lit and unlit plots. These results contrast with previous short-term studies showing dramatic impacts of light pollution on trophic structure.

Introduction

As light pollution—artificial light at night from human activities—becomes increasingly dominant in the nighttime environment (Falchi *et al.* 2016b), greater attention is being given to its ecological effects. Changes in relative abundances of herbivores, predators, parasites, and scavengers within a community (i.e., the community's trophic structure) are important to study because they may signal shifts in the flow of energy and nutrients in a system (Faeth *et al.* 2005), or shifts in the importance of top-down versus bottom-up forces (Bennie *et al.* 2015). Light pollution could alter bottom-up effects if artificial illuminance alters plant phenology or growth. Since light cues in the environment trigger plant flowering and shoot elongation (Parker and Borthwick 1950), illumination from artificial light at night could influence the total amount or seasonal availability of plant resources (Bennie *et al.* 2016), in turn impacting herbivore abundances. Conversely, findings of higher predator abundances near streetlights suggest a strengthening of top-down forces in illuminated areas. For example, Davies *et al.* (2012) and Heiling (1999) reported higher arthropod predator abundances under streetlights. Predators might be attracted to artificial lights, or could be responding to high availability of prey in illuminated areas, as has been reported in insectivorous bats (Rydell 1992). Increased abundance of predatory arthropods could, in turn, increase local predation activities and strengthen top-down pressure on herbivores.

Methodological approaches taken in previous studies of light pollution and arthropod communities limit the inferences that can be drawn from these studies. Much of the evidence for community-level impacts is derived from short-term manipulations, where a light pollution treatment is applied to previously dark habitat over short (less than one week) time periods (Meyer and Sullivan 2013, Perkin *et al.* 2014b). These short-term studies are likely representative of short-term changes in habitat use immediately after a new luminary is turned on, but may not reveal how trophic structure will be impacted over longer time scales.

A second approach common to many previous studies is to compare arthropod communities at different distances from existing luminaries, such as municipal streetlights (Davies *et al.* 2012, Azam *et al.* 2015, Hale *et al.* 2015, Schoeman 2016). However, proximity to municipal streetlights might be associated not only with light levels, but other factors such as amount of pedestrian traffic. Additionally, the focal communities may have already experienced years or decades of nighttime illumination. This makes it difficult to detect variation in community responses over time.

A small number of short-term experimental studies have monitored impacts of light pollution on trophic interactions or community structure over time frames of weeks to months (Bennie *et al.* 2015, Holker *et al.* 2015, Bolton *et al.* 2017). Only one, Bennie *et al.* (2015), does so for a grassland food web. This study found evidence for bottom-up effects of artificial lights. Amber-colored LED lights decreased densities of both flowers and the aphids that fed on them.

Here, I conducted a two-year, manipulative field experiment examining effects of nighttime light pollution on arthropod abundance and trophic structure. Arthropods are an ideal group of organisms for studying light pollution effects on trophic structure. Arthropods occupy a variety of trophic levels, serve as an important food source for many vertebrate predators, and are abundant in landscapes undergoing urbanization (Mcintyre 2000). Studying light pollution effects on arthropod community composition is important from a biodiversity and conservation perspective, but may also signal changes in ecosystem function through changes in trophic composition. Shifts in the relative abundances of predators and their prey may lead to changes in top-down or bottom-up forces within communities, in turn affecting plants and vertebrate predators (Moran and Scheidler 2002, Gruner 2004).

Methods

In May 2015, I established 8 20-m diameter plots in a native grass meadow at Blandy Experimental Farm, a University of Virginia biological research station in the northern Shenandoah Valley of Virginia. The eight 20-m diameter plots were grouped into four pairs, with a 10 m edge-to-edge distance between plots in a pair and a minimum of 20 m between pairs. Within each pair, artificial light at night was added to one randomly chosen plot and the other plot, with no light added, served as a control. Each light post was fitted with either four white LED floodlights (RAB Lighting Bullet 12A; color temperature = 4992 K) or a fake light fixture. Lights were oriented downwards and faced in four different directions to ensure that all four quadrants of the plots were evenly illuminated. The lights were kept on from May 2015-October in 2015 and 2016. A light sensor turned the lights on at dawn and off at dusk. Additional information about the configuration of these plots can be found in the Methods section of Chapter 1.

LED lights were chosen for this study because LED lights are becoming increasingly widespread in residential, municipal, and commercial settings (Stanley *et al.* 2015). Because LED lights emit broadly across the visible spectrum, they are predicted to strongly impact arthropods as lights with broad emittance are more likely to produce light wavelengths overlapping wavelengths arthropods are able to see (Davies *et al.* 2013a). LED lights may also attract more insects than other lighting technologies such as High Pressure Sodium (HPS) owning to high emittance in blue wavelengths overlapping UV-blue-green visual sensitivities of nocturnal insects (Pawson and Bader 2014).

Within each plot, I collected arthropods via sweep net 29 July 2015 and 6 August 2016. Sweep net samples were taken at sunset in 4 m wide x 20 m long, NE-SW transects through the center of each plot. Given the amount of time required to process specimens collected in 2015, I reduced the number of plot transects from two transects in 2015 to one transect in 2016. I froze arthropod specimens immediately after collection, and I later sorted and identified specimens to Order level. I further identified two Orders, Coleoptera and Hemiptera, to Family level. I chose to further identify specimens from these two Orders because these Hemiptera represented a large portion (34%) of the sample and because multiple trophic guilds are potentially represented within Coleoptera and Hemiptera (Price 2011).

I classified the specimens into one of four trophic groups: herbivores, predators, scavengers, or detritovores. I assigned each Coleoptera Family to a single trophic group based on the role ascribed to the majority of its members in Evans (2014). Similarly, I assigned families within Hemiptera to a single trophic group based on literature designations. Hymenoptera and Diptera were included in the analysis of overall arthropod abundance but were not included in the trophic structure analysis because specimens were small (less than 0.1 mm long) and difficult to identify. Orthoptera specimens consisted of grasshoppers (Acrididae) and bush katydids (*Scudderia*), both of which are herbivores. Lepidoptera, Mantodea, and Araneae were assigned to trophic groups based on the feeding guild most common in these groups. Literature sources guiding trophic classification of each taxonomic group are provided in Table 1.

Statistical analysis

I tested light pollution effects on total arthropod abundance using a linear mixed effects model (LME), with light pollution treatment as a fixed effect and plot pair as a random effect nested within sampling year (2015 or 2016). Because I was interested in assessing whether light pollution impacts changes over time, I also performed separate LME models for each year of data collection. I tested light pollution effects on relative abundance within trophic groups using a LME model, with light pollution treatment, trophic group, and the light pollution treatment × trophic group interaction as fixed effects and plot pair as a random effect nested within sampling year. For all analyses, abundance counts were log-transformed to improve the normality of the data distributions and to reduce heterogeneity of variance. Due to low numbers of specimens, scavengers and detritivores, representing 0.01% of the total number of specimens, were excluded from the analysis of trophic structure. I conducted all statistical analyses in R (R Core Team 2015). LME models were performed using the 'lme4' package (Bates *et al.* 2015). P-values were estimated based on type III Satterthwaite approximation for degrees of freedom using the function 'anova' in the 'stats' package (R Core Team 2015).

Results

The 29 July 2015 and 8 August 2016 collections netted a total of 9,925 arthropod specimens; 8,243 specimens in 2015 and 1,682 in 2016. On average, I collected 1,030 ± 141 (1 SE) arthropods per plot in 2015 and 210 ± 34 arthropods per plot in 2016.

In the combined 2015 and 2016 samples, I captured an average of 508 ± 117 arthropods in unlit plots and 739 ± 227 arthropods in lit plots. There was no significant difference in the number of individuals captured in unlit and lit plots for the combined years (Figure 1; $F_{1,10}$ = 2.37, p = 0.15). Twenty-five percent more arthropods were captured on average in lit plots compared to unlit plots in 2015, a marginally significant difference ($F_{1,3}$ = 9.90, p = 0.05). There was no significant difference in the number of arthropods captured in unlit versus lit plots in 2016 ($F_{1,3}$ = 0.06, p = 0.82).

I identified 2,321 Hemiptera and 271 Coleoptera to Family level. I classified 6254 specimens as herbivores, 401 as predators, 2 as detritovores, 4 as scavengers. Although abundances varied across trophic groups, the light pollution treatment × trophic group interaction was not significant (Table 2).

Discussion

I found relatively modest impacts of light pollution on arthropod abundance, and no effect on arthropod trophic structure. Arthropod abundance was 25% higher in lit plots compared to unlit plots, a marginally significant difference, in the first sampling year. However, there was no difference in abundance between lit and unlit plots in the second sampling year.

Light-mediated increases in arthropod abundance in my first sampling year echo findings from other studies examining relatively short (i.e., less than one year) time periods. For example, Davies *et al.* (2012) reported higher abundances of ground-dwelling arthropods under streetlights after 3 nights of illumination. Additionally, Pawson and Bader (2014) found that insect trap capture was 48% higher around LED lights compared to High Pressure Sodium lights left on for 10 days. These results suggest dramatic, short-term increases in arthropod abundances may not reflect long-term changes in local arthropod abundances. One explanation for stronger effects over shorter time scales could be that phototaxic arthropods initially flock to lights from surrounding areas, but over time fewer arthropods immigrate into lit areas as source populations of emigrating arthropods are diminished. This explanation is consistent with the idea of lights creating demographic traps (Chapter 2), or locations where rates of immigration and death exceed rates of emigration and birth.

My results showing no effects of light pollution on trophic structure contrast with previous studies finding dramatic effects of light pollution on densities of predators, prey, or both. Davies *et al.* (2012) found capture of predators and scavengers but not prey increased in pitfall traps under streetlights, and Heiling (1999) reported higher predator and prey densities under lights, but Meyer and Sullivan (2013) reported a 44% decrease in arthropod predator abundance in illuminated areas of a riparian system. Variability of results across studies suggests additional studies should be conducted examining trophic responses to light pollution in a wide range of ecosystems.

My sampling method—sweep netting vegetation at chest height—likely provided a snapshot sample of arthropods present on grasses. It is possible that important changes in trophic structured occurred in other components of the habitat that I did not assess, such as soil or ground-dwelling arthropod assemblages. Additionally, it is possible important changes occurred earlier or later in the growing season, and were undetectable during our sampling window of late July to early August.

I applied a light pollution treatment over 6 months during the growing season for two consecutive years—a long time frame compared to previous studies of impacts of light pollution on trophic structure among arthropods. However, impacts might appear as a result of applying light pollution over even longer time frames than I examined here, particularly if there are impacts on ecosystem dynamics (e.g., nutrient fluxes) that involve delayed feedbacks on arthropods.

The results presented here call for further examination of the causes of light pollution impacts on arthropod communities. First, my results showing temporal variation in light pollution effects on abundance underscore the importance of repeated sampling over long time frames. Second, the short-term increases in abundance in response to light pollution raise questions about the mechanisms underlying this response, i.e., the relative importance of changes in reproduction, mortality, emigration, and immigration. Immigration resulting from behavioral attraction to lights is likely a short-term response, while impacts on birth rates may occur over longer time scales. Quantifying the net influx (immigration - emigration) of arthropods into artificially illuminated habitat as well as local birth and death rates would help resolve the mechanisms whereby light pollution affects local abundance and trophic structure.

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Tables & Figures

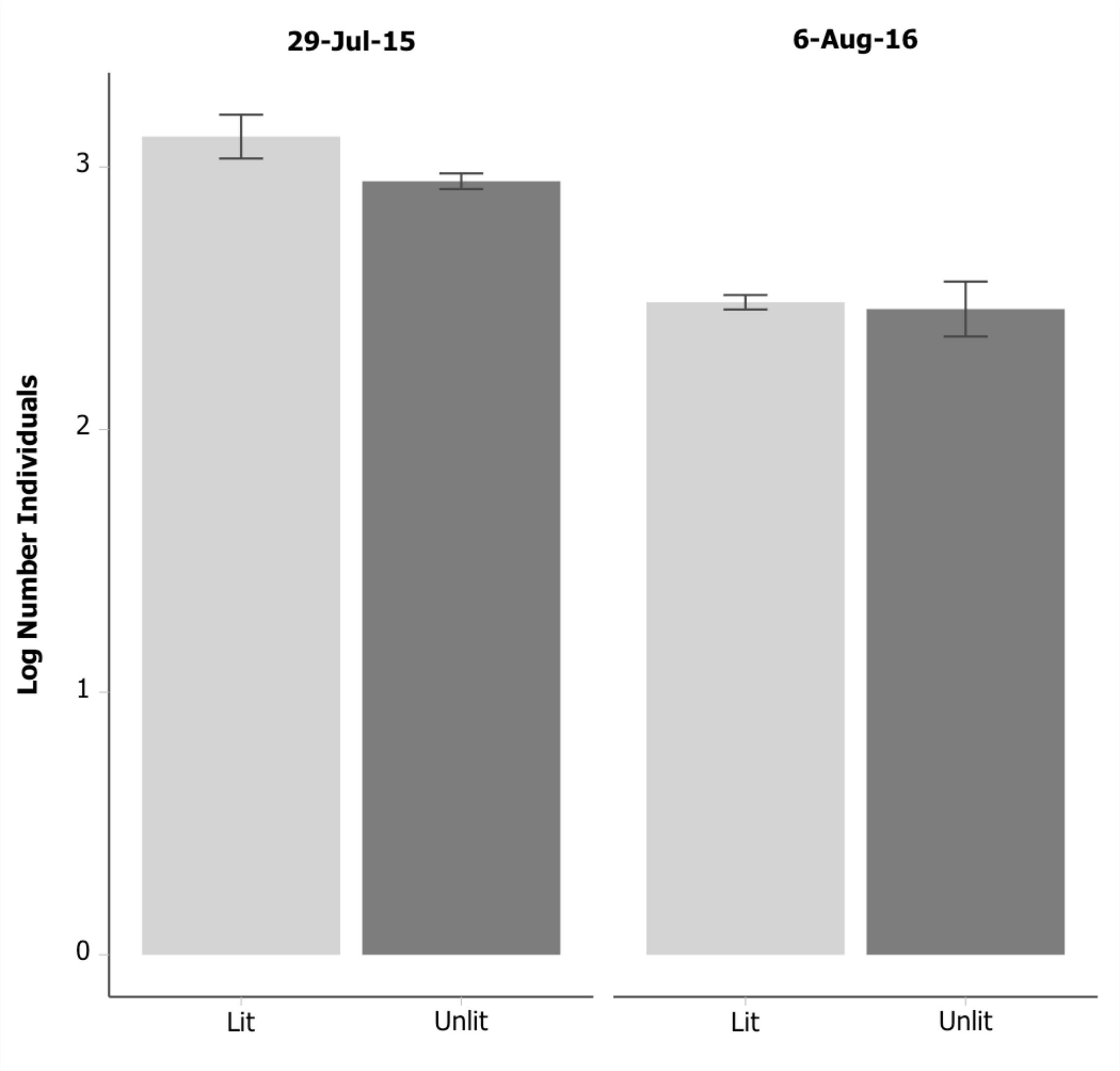

Figure 1. Total number of arthropods captured in experimental field plots randomly assigned to receive artificial night lighting from LED lights or no added light. Error bars represent ± 1 SE.

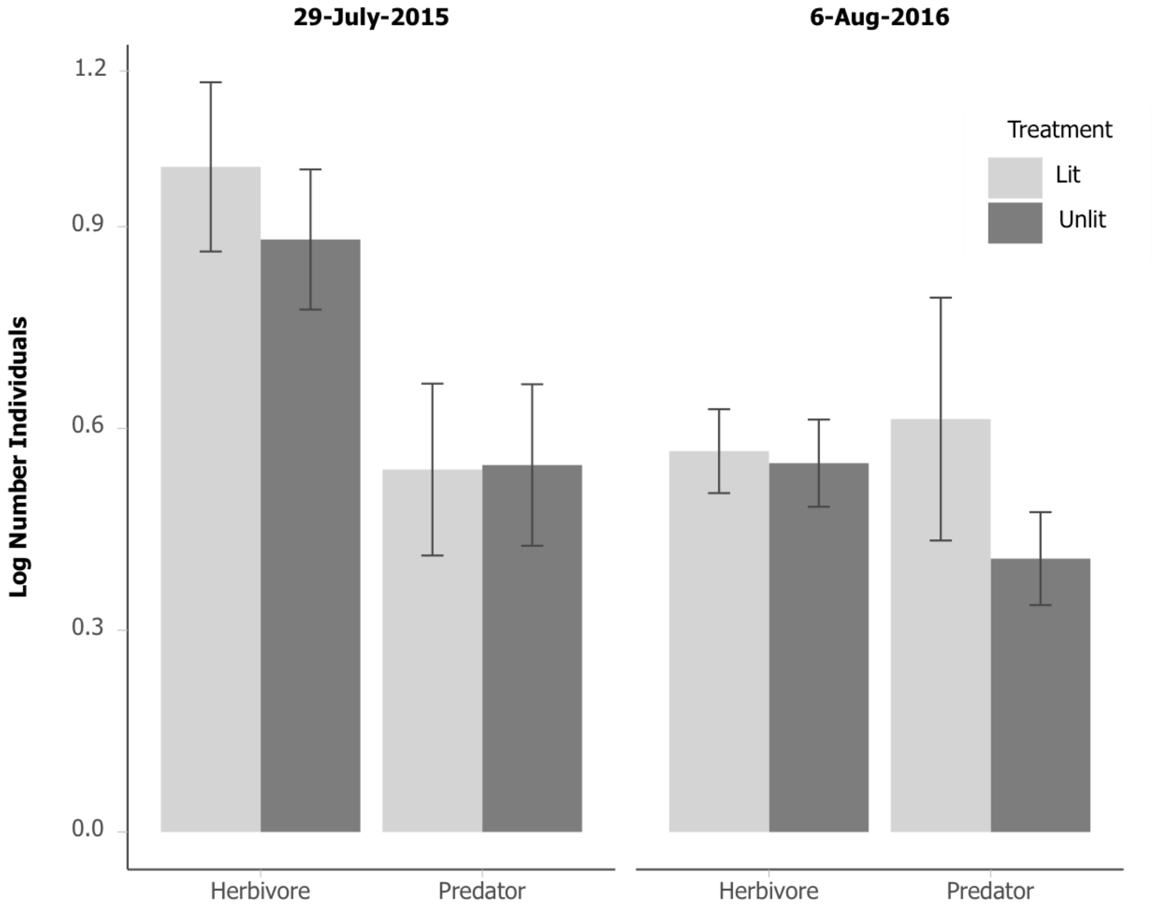

Figure 2. Total number of arthropods captured by trophic group in experimental field plots randomly assigned to receive artificial night lighting from LED lights or no added light. Error bars represent ± 1 SE.

Table 1. Arthropod trophic classifications and literature source.

Group	**Family**	**Trophic Designation**	**Source**
Araneae		Predator	Price 2011
Coleoptera	Anthicidae	Scavenger	Evans 2014
	Cantheridae	Herbivore	Evans 2014
	Carabidae	Predator	Evans 2014
	Chrysomelidae	Herbivore	Evans 2014
	Coccinellidae	Predator	Evans 2014
	Curculionidae	Herbivore	Evans 2014
	Elateridae	Herbivore	Evans 2014
	Histeridae	Predator	Evans 2014
	Latridiidae	Detritivore	Evans 2014
	Nitidulidae	Herbivore	Evans 2014
	Oedemeridae	Herbivore	Evans 2014
	Phalacridae	Herbivore	Evans 2014
	Scarabidae	Herbivore	Evans 2014
	Staphylinidae	Predator	Evans 2014
Hemiptera	Acanaloniidae	Herbivore	Slater and Baranowski 1978
	Cercopidae	Herbivore	Cryan and Svenson 2010
	Cicadellidae	Herbivore	Dietrich 2005
	Lygaeidae	Herbivore	Burdfield-Steel and Shuker 2014
	Nabidae	Predator	Slater 1978
	Pentanomidae	Herbivore	Slater 1978
	Phymantidae	Predator	Slater 1978
	Reduviidae	Predator	Slater 1978
Lepidoptera		Herbivore	Price 2011
Mantodea		Predator	Price 2011
Orthoptera		Herbivore	Price 2011

Table 2. Summary of linear mixed effects model for light pollution treatment × trophic group interaction.

Response Variable	**Sum of Squares**	**Mean Squared Error**	**Numerator df**	**Denominator df**	**F value**	**p value**
Trophic	2.74	2.74	1	252.99	7.92	0.01
Treatment	0.35	0.17	2	253.04	0.50	0.61
Trophic × Treatment	0.87	0.44	2	253.13	1.26	0.28

Conclusions

Recognition of the biological importance of light is hardly new. For example, insect attraction to light has been described for centuries (Graber 1884), as have light effects on plant growth and physiology (Hunt 1844). While light has been a subject of research since practically the dawn of time, light pollution is a relatively new phenomenon in its current manifestation (Bogard 2013). Light pollution's large and growing extent overlaps huge swaths of the globe and species' ranges therein (Bennie *et al.* 2014, Falchi *et al.* 2016a). In this new era of widespread illumination of the night, isolating light pollution impacts on organisms and populations is complicated by the spatial association between light pollution, urban land cover, and the suite of other stressors associated with urbanization (Sutton 2003, Halfwerk and Slabbekoorn 2015). A combination of manipulative field experiments, such as those described in Chapters 1, 2, and 4, as well as surveys across large areas, such as those described Chapter 3, is one potentially promising approach to distinguish the effects of light pollution from those from other stressors, ultimately allowing stakeholders to make informed decisions regarding the management of light pollution across landscapes.

In this dissertation, I described light pollution impacts on firefly courtship behavior, mating, movement, and distributions. Because firefly flashes are intimately linked with mating and fitness (Cratsley and Lewis 2003, Lewis and Cratsley 2008), findings that light pollution interrupts firefly flash dialogues (Chapters 1-2) suggests light pollution may represent a stressor for firefly populations, an idea for which I find additional evidence in the negative association between light pollution and firefly abundance across large areas (Chapter 3).

The work presented in this dissertation includes some of the first field-based manipulative experiments examining light pollution's effects on population abundance and community composition in the field. I delved into mechanisms underlying impacts on abundance (e.g., attraction and reduced mating)—a step still uncommon in the literature. I also present one of the only surveys of fireflies on residential properties in eastern North America, leading to a unique comparison of scientist- and citizen scientist-collected data.

Light pollution may be contributing to the decline of nocturnal insects. In a recent ground-breaking study, Langevelde *et al.* (2018) showed populations of nocturnal, light-attracted moths disproportionality declined in the past 30 years compared to populations of diurnal or aphototaxic moths, and named light pollution as the primary factor contributing to these declines.

It is difficult to similarly assess the health of firefly populations in North America due to the paucity of long-term, spatially-detailed datasets. Anecdotally, many firefly enthusiasts believe fireflies are disappearing. “You never see fireflies anymore,” is a refrain I heard again and again from homeowners during my survey of fireflies in Virginia in 2017. In the absence of long-term data on firefly populations in North America, it is difficult to affirm or refute these impressions. Given the numerous potential stressors associated with urbanization, such as habitat loss from land cover change, pesticides, and light pollution, the inference that firefly populations are vulnerable is not outlandish. Citizen science programs such as Firefly Watch will likely play an invaluable role monitoring firefly populations going forward. My analysis showing comparable findings in datasets collected by a professional scientist and by citizen scientists suggest that these citizen science data may provide a good window into the status of firefly populations across large areas.

My research also highlights the need for continued work assessing light pollution impacts on arthropod communities more broadly. In chapter 4, I showed light pollution impacts on arthropod communities, such as changes in abundance, varied over the 2 years of the study. Differences in community responses over time underscore the need for additional long-term studies, which are largely lacking in the literature thus far. Because arthropods are diverse, abundant in urbanizing landscapes (McIntyre 2000), and play a key role in terrestrial food webs (Yang and Gratton 2014), light pollution impacts on arthropods will likely ripple through ecosystems, with repercussions for species interactions, ecosystem services such as pollination, and nutrient cycling.

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