Multi-year experiment shows no impact of artificial light at night on arthropod trophic structure or abundance

Ariel Firebaugh1 AND Kyle J. Haynes2,3

1Biology Department, Radford University, Radford, Virginia 24141 USA
2Department of Environmental Sciences, University of Virginia, Charlottesville, Virginia 22904 USA
3Blandy Experimental Farm, University of Virginia, 400 Blandy Farm Lane, Boyce, Virginia 22620 USA

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Abstract. Prior studies of how artificial light at night (ALAN) alters the abundances of herbivores, predators, and other trophic groups have yielded evidence of the alteration of energy and nutrient flows through ecosystems. Because the impacts of ALAN on arthropod assemblages may be context-dependent, there is a need for more experimental work across a range of habitat types and time frames. To examine longer-term impacts of ALAN on community and trophic structure, we experimentally manipulated ALAN in a grassland ecosystem and compared arthropod abundance and trophic structure between plots exposed to ALAN and plots exposed only to ambient light over two years. In 2015, arthropod density was 61% higher in plots with ALAN added than in plots with no ALAN added, but this difference was not statistically significant. In 2016, arthropod densities were nearly identical between plots with ALAN added and plots not exposed to ALAN. Contrasting with prior research on ground-dwelling arthropods, we found no evidence that the effects of ALAN on abundance differed between herbivores and predators inhabiting the canopy of grassland vegetation. To better understand the ecological consequences of ALAN, we recommend experimental manipulation of ALAN in a variety of habitat types followed by repeated sampling of trophic structure over time frames that span multiple generations for the species within the focal community.

Key words: community; food web; insects; light pollution; sensory pollutant; spiders; terrestrial.

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† E-mail: kjh8w@virginia.edu

INTRODUCTION

As artificial light at night (hereafter ALAN) becomes increasingly bright and pervasive (Falchi et al. 2016), greater attention is being given to its ecological effects. Human-induced changes in the relative abundances of herbivores, predators, parasites, and scavengers within a community (i.e., the community’s trophic structure) 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. For example, in experimental mesocosms, Bennie et al. (2015) found that ALAN, through direct effects on rates of flowering, altered herbivore abundance through bottom-up effects. Conversely, in an observational field study, Davies et al. (2012) found higher abundances of predaceous and scavenging arthropods directly underneath streetlights than between streetlights, but no such effects on densities of grazers or other trophic groups, suggesting that top-down forces may increase with the intensity of ALAN.

Much of the evidence from field studies on how ALAN impacts trophic structure in arthropods is derived from manipulations where an ALAN treatment was applied to previously dark habitat over time periods of less than one
growing season (1–4 months; Meyer and Sullivan 2013, Perkin et al. 2014, Sullivan et al. 2019). Although arthropods can exhibit ALAN-induced dietary shifts over these same timescales (Sullivan et al. 2019), some portion of the effects of ALAN on trophic structure in these studies may be attributed to short-term changes in habitat use. The consequences of ALAN for arthropod trophic structure over timescales that span several generations for the respective species (e.g., multiple years for univoltine insects) might be more or less dramatic depending on how ALAN alters a variety of slow-acting or delayed processes such as reproductive success and temporal density dependence in population growth or propagation of effects through multiple trophic levels. For example, the local abundances of species exhibiting positive phototaxis might initially increase around sources of ALAN that are added to habitat previously free of ALAN, but the positive effect on local abundance could potentially attenuate over time if ALAN increases rates of mortality (Eisenbeis 2006) or decreases rates of reproduction (Firebaugh and Haynes 2019).

With their surveys of ground-dwelling arthropods under and between existing municipal streetlights, Davies et al. (2012) showed that ALAN can influence trophic structure long after ALAN has been introduced. Multi-year field experiments, on the other hand, have revealed that the impacts of ALAN impacts on arthropod communities can change over time. In a three-year field experiment, Davies et al. (2017) found that spider abundances were higher in plots exposed to certain ALAN regimes compared to plots receiving only ambient light for the first two years of the experiment, but there were no effects on spider abundances in the third year of the study. In contrast, predatory beetles were more abundant in some ALAN treatments only in the third year of the study. In a study using a before-after-control-impact design in a riparian system, Manfrin et al. (2017) found ALAN reduced abundances of predatory ground-dwelling arthropods one year after ALAN was added, but not within the first year that ALAN was added. These studies illustrate the importance of examining the effects of ALAN on arthropod communities over long timescales.

Here, we conducted a manipulative field experiment examining effects of ALAN on arthropod density and trophic structure over a period of two growing seasons. Previous field experiments examining effects of ALAN on arthropod assemblages have been carried out in riparian systems (e.g., Perkin et al. 2014, Manfrin et al. 2017), forest edges (Spoelstra et al. 2015), or mown grassland dominated by cool-season (C3) species (e.g., Davies et al. 2017). In contrast, our experiment was carried out in an unmown grassland dominated by warm-season (C4) grasses. Additionally, whereas previous studies of effects of ALAN on arthropod assemblages have primarily examined effects on flying insects, emerging aquatic insects, and/or ground-dwelling arthropods, our study examined effects on arthropods collected from grassland vegetation via sweep netting.

We expected that the addition of ALAN to an ALAN-naive grassland would lead to local increases in arthropod density. However, given that many insects attracted to ALAN are thought to suffer increased mortality, and that attraction of insects toward lights could lead to depletion of surrounding source populations over time (Eisenbeis 2006), we thought that initial increases in density in plots where ALAN was added might fade over time. However, due to the lack of knowledge about how the different groups of arthropods that occupy warm-season grassland vegetation respond to ALAN, we made no predictions about how ALAN would affect trophic structure.

We compared arthropod density and trophic structure between field plots exposed to ALAN from white LEDs and plots not exposed to ALAN. Broad-spectrum light-emitting diodes (LEDs) were chosen for this study because they are becoming increasingly widespread in residential, municipal, and commercial settings (Stanley et al. 2015). The transition from older narrow spectrum lighting technology (e.g., sodium vapor lights) to broad-spectrum lighting technologies increases the ability to detect objects in broad range of animal taxa, but also might alter species interactions as the transition in lighting spectra increases disparities among trophic groups in visual ability (Davies et al. 2013). In addition, Pawson and Bader (2014) found that more insects are attracted to broad-spectrum LEDs than narrow spectrum lighting.
METHODS

Our experiment was carried out in the Native Plant Meadow (NPM) at Blandy Experimental Farm (BEF), a 300-ha environmental research station owned by University of Virginia. The landscape of BEF consists of 120 ha of pasture and cropland, 80 ha of successional old fields, a 60-ha arboretum, 40 ha of woodland, and ponds and wetlands (Bowers 1997, Aneece and Epstein 2015). The 10-ha NPM, where the experiment was conducted, was planted in 2000 and lies roughly in the center of BEF. The NPM is dominated by native warm-season (C4) grasses including switchgrass (Panicum virgatum), Indian grass (Sorghastrum nutans), and big bluestem (Andropogon gerardii). Encroachment of shrubs and trees into the NPM is prevented primarily via controlled burns, with each section burned once every three years in early spring or late fall, and secondarily through targeted application of herbicides on certain invasive shrub species. Insecticides are used occasionally within the arboretum at BEF to treat pest outbreaks on affected shrub or tree species, but they are not used in the NPM or BEF’s successional old fields or woodlots and they have not been used in BEF’s pasture or cropland during or since 2001 (their use prior to 2001 in BEF’s pasture and cropland is unknown).

In May 2015, we established eight 20-m diameter plots in the NPM. The eight plots were grouped into four pairs, with a 10 m edge-to-edge distance between plots in a pair and >20 m between pairs. Within each pair, ALAN was added to one randomly chosen plot and the other plot, with no ALAN added, served as a control. Each light post was fitted with either four white (color temperature = 4992 K) 12 W LED floodlights (Bullet, RAB Lighting, Northvale, New Jersey, USA) or a fake light fixture at a height of 3 m above the ground. The emission spectrum of this LED, which we measured with a STS-VIS-L-50-400-SMA Ocean Optics spectrometer (Largo, Florida, USA), is provided in electronic supplementary material (Appendix S1). An LED was placed on each of the four sides of the 3.7 × 8.5 cm light post to ensure that all four quadrants of the plots were evenly illuminated. Each LED pointed downwards, ~25° outward from the vertical plane of the light post. The lights were kept on from May-October during both 2015 and 2016. A light sensor turned the lights on at dawn and off at dusk. We measured illuminance in each plot 0, 2, 5, 10 m away from the light post by holding a light meter (Extech LT300) at a height of 1 m above the ground on a cloudless night with a new moon. Illuminance was 98.62 ± 4.15 (mean ± SD) lux in the plots where ALAN was added and 0.02 ± 0.01 lux in the plots with ambient light only. Data on variation in illuminance as a function of distance from the central light post are shown in Fig. 1 of Firebaugh and Haynes (2016).

Within each plot, we collected arthropods from the aboveground vegetation via sweep net 29 July 2015 (a waxing gibbous; close to a full moon) and 6 August 2016 (a waxing crescent; close to a new moon). Although the differences in lunar phase between sampling periods are not ideal, because, for example, lunar phase can influence the number and composition of flying insects captured in light traps (e.g., Bowden and Church 1973, Taylor 1986), for our study of
arthropods collected from grasses, we felt that collecting during the same lunar phase each year was likely less important than sampling at the same time of year to avoid biases caused by seasonal variation in taxonomic structure and trophic composition. Sweep net samples were taken two hours after sunset in 2 m wide NE-SW transects through each plot. The specimens were preserved by freezing immediately after collection. Given the large amount of time required to process specimens collected in 2015, we reduced the number of transects in each plot from two parallel 20 m long (80 m$^2$) transects in 2015 to one 20 m long (40 m$^2$) transect that passed directly through the center of the plot. We corrected for differences in the area sampled between 2015 and 2016 by dividing the numbers of arthropods captured by the area (m$^2$) sampled in a given year.

We taxonomically classified the specimens for the purpose of assigning them to different trophic groups (herbivores, predators, scavengers, or detritivores). While in some cases we were able to assign a specimen to a trophic group based on its order (Lepidoptera, Mantodea, and Araneae), a Coleoptera, Hemiptera, or Orthoptera specimen was assigned to a trophic group based on its family or genus (some Orthoptera). We assigned each taxon to a single trophic group based on the role ascribed to the majority of its members in literature sources (Table 1). Because their small size (<1 mm) made classification to family or lower taxonomic level difficult, Hymenoptera and Diptera specimens were not assigned to trophic groups. All specimens, including those not assigned to a trophic group, were included in analyses of overall arthropod density (number/m$^2$).

### Statistical analyses

We intended to test whether effects of ALAN on arthropod density (number/m$^2$) varied over time in a repeated-measures analysis using a linear mixed effects (LME) model; however, such models would not converge properly. A simpler approach was used as a replacement. For each year, we tested whether ALAN affected arthropod density using paired t-tests.

We tested whether ALAN impacted densities in different trophic groups differently in a repeated-measures analysis using an LME model, with ALAN, year, trophic group, and the ALAN × trophic group interaction as fixed effects, and the random effect of plot pair across years as uncorrelated random intercepts and slopes. Densities were Box-Cox transformed using a value for the exponent ($\lambda$) of $-0.16$ to improve the normality of the model residuals. Due to low numbers of scavenger and detritivore specimens (0.05% of the total number of specimens), these two trophic groups were excluded from the analysis of trophic structure. Thus, our analysis examined whether ALAN had differential effects on the densities of herbivores versus predators.

We conducted all statistical analyses in R (R Core Team 2015). The LME models were performed using the lme4 package (Bates et al.

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### Table 1. Arthropod trophic classifications and literature sources.

| Order          | Family       | Trophic Designation | Source                      |
|----------------|--------------|---------------------|-----------------------------|
| Araneae        | Anthicidae   | Predator            | Price (2011)                |
| Coleoptera     | Anthicidae   | Scavenger           | 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)                |
| Scarabaeidae   | Herbivore    |                     | Evans (2014)                |
| Staphylinidae  | Predator     |                     | Evans (2014)                |
| Hemiptera      | Acanaloniida | 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)               |
|                | Pentatomidae | Herbivore           | Slater (1978)               |
|                | Phymantidae  | Predator            | Slater (1978)               |
|                | Reduviidae   | Predator            | Slater (1978)               |
| Lepidoptera    | Herbivore    |                     | Price (2011)                |
| Mantodea       | Predator     |                     | Price (2011)                |
| Orthoptera     | Acrididae    | Herbivore           | Price (2011)                |
|                | Tettigoniidae| Herbivore           | Price (2011)                |
The lmerTest package was used to obtain p-values (Kuznetsova et al. 2016) using Satterthwaite’s method.

**RESULTS**

The 29 July 2015 and 6 August 2016 collections yielded a total of 9,925 arthropod specimens; 8,243 specimens in 2015 and 1,682 in 2016. We collected an average of 12.88 ± 5.0 (1 SD) arthropods per m² in 2015 and 5.25 ± 2.44 arthropods per m² in 2016. In 2015, densities of arthropods were 61% higher, on average, in plots exposed to ALAN compared to the unlit controls, but this difference was not significant (Figure 1, mean difference = 6.04, t₃ = 2.89, P = 0.06). In 2016, arthropod densities were nearly identical between plots exposed to ALAN and plots with no ALAN added (mean difference = −0.15, t₃ = −0.07, P = 0.95).

We classified 6,254 specimens as herbivores, 401 as predators, two as detritivores, and four as scavengers. Herbivore, but not predator, densities tended to be slightly higher in plots exposed to ALAN than in plots exposed only to ambient light (Figure 2), but the effects of ALAN did not differ significantly between herbivores and predators based on the test of the ALAN × trophic group interaction (Table 2).

**DISCUSSION**

Several studies of ground-dwelling and flying arthropods have revealed effects of ALAN on arthropod abundance and taxonomic composition (e.g., Perkin et al. 2014, Davies et al. 2017, Manfrin et al. 2017), but effects on trophic structure have also been documented. Davies et al. (2012) and Sullivan et al. (2019) both found higher abundances of ground-dwelling predators under ALAN. For example, Davies et al. (2012) captured higher numbers of predators and scavengers but not prey under municipal streetlights. In contrast, in our captures of arthropods from within the canopy of tall grasses, we did not find a significant effect of ALAN on trophic structure (P = 0.58; Table 2, Fig. 2). It is possible this inconsistency is due to ALAN having stronger effects on trophic structure in ground-dwelling arthropods than in arthropods inhabiting grassland canopy, but more research is needed to resolve this question.

Our capture method, sweep net sampling, and the time of day it was carried out, two hours after sunset, likely influenced the types of arthropods we were most likely to capture. Although these collections were carried while the plots were being exposed to ALAN, as the lights turned on at sunset, this approach may have favored capturing diurnal species and herbivores perched on vegetation over nocturnal and ground-dwelling species. Studies comparing sampling techniques in grassland systems have found that...
sampling technique impacts arthropod capture. For example, Spafford and Lortie (2013) found that pan traps collected more Collembola and Hymenoptera, while sweep net sampling captured more arachnids. Doxon et al. (2011) found that sweep net sampling captured larger insects and more Orthoptera, Homoptera, and Araneae than vacuum sampling. Studies of ALAN impacts on ground-dwelling arthropods have typically used pitfall traps (Davies et al. 2012, 2017), while a study of the effects of ALAN on attraction of flying insects used flight-intercept (sticky) traps (Pawson and Bader 2014). In riparian systems, in particular, researchers have examined effects of ALAN on arthropod assemblages using combinations of different collection methods including floating emergence traps, pitfall traps, and flight-intercept (air elecotor) traps (e.g., Perkin et al. 2014, Manfrin et al. 2017). Studies employing a variety of collection methods are likely to yield the most comprehensive information on the effects of ALAN on arthropod assemblages given that each collection method is likely to favor capture of arthropod groups occupying a particular type of microhabitat (e.g., ground vs. vegetation canopy) or displaying a particular mode of locomotion (e.g., crawling vs. flying).

Regarding the hypothesis that effects of ALAN on arthropod abundance would be strongest initially and weaken over time, arthropod density was, on average, 61% higher in plots exposed to ALAN compared to unlit controls in the first year of the experiment (2015) but nearly identical between treatments in 2016 (Fig. 2). However, we detected no significant effects of ALAN on arthropod density in 2015 ($P = 0.06$) or 2016 ($P = 0.95$). Given the low replication in our experiment ($n = 4$), it would be premature to reject the hypothesis that impacts of ALAN on arthropod abundance change over time.

We recommend that experimental manipulation of ALAN be followed by repeated sampling of abundance and trophic structure over time frames that span multiple generations. A three-year experiment carried out by Davies et al. (2017) revealed striking differences in the effects of ALAN on species composition within beetle and spider assemblages across years. Similar long-term studies examining effects on trophic structure across a broader set of taxa and habitat types, particularly if they could incorporate investigation of ALAN-induced changes in diet (e.g., Sullivan et al. 2019) at various trophic levels, would substantially advance our understanding of the impacts of ALAN on community structure and dynamics through time.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3227/full