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# Impact of Light Pollution on Species Interactions

## Abstract

Over half of the world's population lives in urban areas leading to night skies that are substantially degraded by artificial lights. Yet, we know little about how light pollution affects the surrounding natural communities. What we do know focuses on the impact of light pollution on individual species. Therefore, I investigated the impact of light pollution on species interactions. I determined whether light pollution is a mechanism of community change, evaluated whether there were changes in species interactions between predators and prey, and indirect and direct interactions between insect herbivores and their host plants by examining the entire life cycle of nocturnal Lepidoptera (moths). Ultimately, I found that light pollution induces an ecological trap for moths.

I evaluated the importance of light pollution in structuring moth communities by collecting moths from a wide variety of prairie fragments with different habitat sizes, vegetation, and light pollution levels to determine if there are any changes in abundance, richness, and composition of the lepidopteran community in response to these variables. I found that light pollution changes the abundance, richness, and composition of moth communities. Notably, my research indicates that direct sources of light pollution, such as streetlights, may have different consequences on nocturnal lepidopteran communities than night skies degraded from indirect "skyglow".

To determine potential mechanisms underlying these patterns and whether or not light pollution acts as an ecological trap, I also completed two projects to test the fitness costs of light pollution on moths at the larval stage. I found that nocturnal generalist predators do not forage preferentially for larvae in streetlit or unlit areas along suburban prairie fragments. However, light pollution induces direct consequences for larvae and indirect negative effects on larvae mediated through changes to host plant quality induced by light pollution.

My research determined that more moths and species are attracted to sites with high levels of light pollution. I also determined that there are negative consequences at the larval stage to living in illuminated areas that are mediated through species interactions. Therefore, light pollution creates an ecological trap for moths.

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IMPACT OF LIGHT POLLUTION ON SPECIES INTERACTIONS

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A Dissertation

Presented to

the Faculty of Natural Sciences and Mathematics

University of Denver

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In Partial Fulfillment

of the Requirements for the Degree

Doctor of Philosophy

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by

Kylee Grenis

June 2016

Advisor: Shannon M. Murphy

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Author: Kylee Grenis

Title: IMPACT OF LIGHT POLLUTION ON SPECIES INTERACTIONS

Advisor: Shannon M. Murphy

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### **Abstract**

Over half of the world's population lives in urban areas leading to night skies that are substantially degraded by artificial lights. Yet, we know little about how light pollution affects the surrounding natural communities. What we do know focuses on the impact of light pollution on individual species. Therefore, I investigated the impact of light pollution on species interactions. I determined whether light pollution is a mechanism of community change, evaluated whether there were changes in species interactions between predators and prey, and indirect and direct interactions between insect herbivores and their host plants by examining the entire life cycle of nocturnal Lepidoptera (moths). Ultimately, I found that light pollution induces an ecological trap for moths.

I evaluated the importance of light pollution in structuring moth communities by collecting moths from a wide variety of prairie fragments with different habitat sizes, vegetation, and light pollution levels to determine if there are any changes in abundance, richness, and composition of the lepidopteran community in response to these variables. I found that light pollution changes the abundance, richness, and composition of moth communities. Notably, my research indicates that direct sources of light pollution, such as streetlights, may have different consequences on nocturnal lepidopteran communities than night skies degraded from indirect "skyglow".

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# CHAPTER ONE: IMPACT OF LIGHT POLLUTION ON COMMUNITIES OF NOCTURNAL LEPIDOPTERA

## Introduction

More than half of the world's population lives in urban or suburban areas (McIntyre et al. 2001) and this development has caused nearly 20% of the Earth's night skies to be affected by anthropogenic light (Cinzano, Falchi, and Elvidge 2001; Kyba et al. 2011). At night, these artificial lights function to extend human activities and promote safety (Painter 1996). However, we rarely consider the consequences of artificial lights on species adjacent to urban areas. Furthermore, most studies of light pollution focus on individual species and lack an ecological community perspective (Gaston, Visser, and Hölker 2015). Recently there have been several calls in the literature for studies that investigate how the effects of light pollution vary among species and associated effects on populations, communities, ecosystems, and species interactions (Gaston, Visser, and Hölker 2015; Hölker, Wolter, et al. 2010; Hölker, Moss, et al. 2010; Lyytimäki 2013; Gaston et al. 2013; Macgregor et al. 2014). What we do know about light pollution primarily comes from case studies on vertebrates, such as bats, birds, turtles and humans (Rydell, 1992, 2006; Rich & Longcore, 2006; Navara & Nelson, 2007; Santos *et al.*, 2010; Jung & Kalko, 2010; Kempenaers *et al.*, 2010; Falchi *et al.*, 2011; Bedrosian & Nelson, 2013; Davies *et al.*, 2013; Gaston *et al.*, 2013; Kamrowski *et al.*, 2014; Da Silva

*et al.*, 2015; Hale *et al.*, 2015 and references therein; but see Davies *et al.*, 2012, 2013; Bennie *et al.*, 2015). Additionally, studies focus primarily on the impacts of light pollution measured as a categorical variable (light or no light) when quantitative measures, like illuminance and luminance, of artificial light are available.

Frequent exposure to long periods of uninterrupted light has varying impacts on species (Longcore and Rich 2004). Some species, like spiny mice for example, require the dark to forage successfully (Rotics, Dayan, and Kronfeld-Schor 2011) while other species can extend their foraging due to artificial light, as is the case for some shorebirds (Santos *et al.* 2010). Other species use naturally occurring light, like moonlight or starlight at night, to navigate; artificial lights can mimic that light and cause species to make maladaptive decisions based this on formerly reliable cue. For example, hatchling sea turtles will navigate towards artificial lights near cities rather than towards moonlight reflected off the ocean leading to increased juvenile mortality (Tuxbury and Salmon 2005). This particular example of the effects of light pollution on an individual species is also known as an ecological trap.

Ecological traps are formally defined as anthropogenic changes in the environment that cause organisms to make decisions based on formerly reliable cues that now negatively affect their fitness (Schlaepfer, Runge, and Sherman 2002). When an ecological trap is created, the vast majority of individuals will actively choose low-quality habitat because it exhibits cues typical of high-quality habitat that were formerly reliable. Organisms may use low-quality habitat because of reduction of quality in high-quality habitats where the original cue exists, low-quality habitats exhibiting increased cues of high-quality habitat, or a combination these factors. Although these shifts in

habitat quality can occur in undisturbed landscapes as well, they are specifically considered ecological traps if the alterations in the environment are human induced. Under natural regimes, large scale environmental changes usually occur over evolutionary time, which allows time for populations to adapt (Schlaepfer, Runge, and Sherman 2002; Robertson and Hutto 2006; Kristan 2003; Battin 2004); however, the term ‘ecological trap’ more appropriately attributes this new maladaptation directly to human impacts in an ecological time frame that can drastically reduce population sizes (Schlaepfer, Runge, and Sherman 2002; Battin 2004; Kristan 2003; Robertson and Hutto 2006). Artificial lights often mimic the moon, causing species to mistakenly use the artificial lights as a cue, thus creating an ecological trap. If light pollution has significant effects on individual species, like inducing ecological traps, it follows that it may have important implications for community dynamics by altering entire community composition.

It is already known that light pollution is causing evolutionary change in moths, but we do not know how it is impacting entire communities (Altermatt and Ebert, 2016). To our knowledge, only three studies have investigated how moth community abundance and species richness are affected by landscape-level anthropogenic disturbances like habitat fragmentation (Summerville and Crist 2004; Fuentes-Montemayor et al. 2012; Ricketts et al. 2001). Notably, all of these studies occurred within forest fragments surrounded by agricultural fields, not urban development which introduces new and different pressures, like light pollution.

These studies however, did not detect the typical species-area pattern commonly found for other organisms in which species richness decreases with habitat size like butterflies (Robinson, Armstead, and Bowers 2012), bees (Hinnners, Kearns, and Wessman 2012), and grasshoppers (Nufio, McClenahan, and Bowers 2010), tested in our same study location. Instead, studies on moths found that moth communities respond more predictably to plant richness (Ricketts et al. 2001; Summerville and Crist 2004). Most herbivorous insects are specialists that feed exclusively on a single plant species or several closely related species (Price et al. 2011). Increases in plant diversity within a habitat patch positively affect moth species richness (Summerville and Crist 2004; Fuentes-Montemayor et al. 2012), but vegetation diversity is not always dependent on patch size, particularly in urban and suburban landscapes (Lindenmayer and Fischer 2006; Hinnners, Kearns, and Wessman 2012; Jules and Shahani 2003). It is therefore important to account for possible influences of vegetation on moth communities. All of these patterns have yet to be confirmed in either a prairie ecosystem or an urban-suburban dominated matrix where moths are exposed to artificial light.

It is well known that moths are attracted to artificial lights and light pollution is implicated as a reason for 27-31% declines in moth species richness the last 50 years (Fox 2013) but has yet to be empirically tested. There is evidence that light pollution has negative impacts on moth individuals (Frank 1988). For example, moths attracted to artificial lights are subject to more predation by insectivores like bats and birds (Rydell 1992) and suffer from reduced vision capabilities after exposure to streetlights (Mizunami 1995). There are also potential negative impacts yet to be tested, like fitness costs to light attraction; for example, moths circling lights may suffer from reduced



energy stores or may not be able to find suitable oviposition sites, resulting in smaller larvae developing under streetlights (Grenis and Murphy, in prep). With all these negative impacts of artificial lighting, both documented and potential, artificial light could be an ecological trap that leads to changes in moth communities.

Our study tests the hypothesis that light pollution can cause shifts in community composition of species reliant on nocturnal light cues. Specifically, we test whether habitat fragmentation and light pollution affect communities of moths in shortgrass prairie patches. We predict that sites with high levels of light pollution will lower both moth abundance and species richness and alter the community composition of moths.

## **Materials and Methods**

### **Study System**

In this study, we surveyed moth communities at 23 prairie fragments along the Front Range of Colorado, USA. We selected sites in four general areas in the Denver-metro area across five counties (Appendix Table B1). We chose sites bordered by at least 75% residential/suburban development around the site circumference. The native ecosystem in the sites is shortgrass steppe with infrequent patches of tallgrass and native trees along riparian and mesic areas. Annual precipitation for this region is about 400mm and local elevation ranges between 1540 m and 1788 m. In order to make sure that sites were not lumped by size and to have a representative sample of habitat sizes, each county contained at least five fragments with one small site (<5ha), three to five medium sites (5-15ha), and one large site (>15ha). Overall, site areas ranged between 2.42 ha and 73.66 ha. We determined site area using digital data from city and county records.

Because previous studies have shown that moth communities are dependent on vegetation present, we included a vegetation measure as a variable in our study. We used ground cover measures instead of vegetation diversity because of the difficulty in identifying prairie grasses to species before and after flowering. To account for vegetation in our survey, we measured the proportion of the ground covered by grasses, forbs, and bare ground every 0.3 meters across five point-intercept line transects at each site. Transects spanned the longest North-South and East-West distances in each site (Appendix Figure B1). We also measured ground cover at a three meter radius (18.85m circumference) surrounding each trap location to account for vegetation within trap attraction range (Baker and Sadovy 1978) (Appendix Figure B1). To account for differences in site area and shape, we used proportion ground cover to standardize measurements for analyses.

Longcore and Rich (2006) recommend quantifying the amount of artificial light present in the environment as both illuminance and luminance. Assessing both measurements is common practice in other disciplines interested in artificial lighting, and the two measure different aspects of artificial night lighting. Illuminance is defined as the luminous flux incident on an area with a standard SI unit of lux; in other words, illuminance measures the brightness of a point source of light. We measured illuminance to the nearest 0.01 lux using an Extech EA33 Luxmeter (Extech Instruments Corporation, Nashua, NH, USA). Luminance is the intensity of light per unit area of its source with a standard SI unit of candela (cd)/m<sup>2</sup>; luminance can be described as how bright objects appear or how much light is reflected off an object. We measured luminance to the 0.01 magnitudes per square arcsecond using a Sky Quality Meter (Unihedron, Grimsby,

Ontario, Canada) and converted later to the SI unit  $\text{cd/m}^2$ . To measure relative light levels across the entire site, we measured illuminance and luminance at 29 positions at each site with 24 positions along the edge and 5 in the center and averaged them together (Appendix Figure B1). We took measurements after astronomical twilight on clear nights within three days before and after the new moon between the hours of 20:00 and 02:00 to reduce the influence of natural light on our measures.

### Survey Methods

To characterize the moth communities at each site, we sampled moths on nights without rain or gusting winds and with less than one hour of natural moonlight between 20:00 and 02:00 during 5 collection periods over the summers of 2011 and 2012. However, we did not sample all sites in all collections due to weather, permitting, and safety (Appendix Table B1). We sampled sites haphazardly based on county location so that multiple sites could be visited in the same night. To sample moth abundance and diversity, during each survey we used two Universal Black Light Traps (Bioquip Products, Rancho Dominguez, CA, USA) to collect moths. To ensure that we sampled the moths in the entire community rather than just those attracted to lights and to minimize the degree to which the traps competed with nearby streetlights, we placed each trap at least 15m from the edge of the site. During collection periods in July and August of 2011 and June of 2012, we visited traps every other hour and emptied them. After collection, we froze and stored all the collections in the laboratory until we could count, pin, and identify macromoths to species with the assistance of local taxonomic experts

(D. Bettman & C. Harp). We vouchered specimens in the Zoology collections at the Denver Museum of Nature and Science.

### Statistical Analyses

To evaluate differences in species richness and abundance, we used two multiple regressions with site area, proportion grass, illuminance, and luminance as independent variables. We used a log transformation to get site area to conform to the assumption of normality and a square root transformation to get illuminance and luminance as close to normal distribution as possible. We used the average of the abundance-based coverage estimator (ACE), the incidence-based coverage estimator (ICE), and the first order Jackknife to estimate the number of species that remained undiscovered (Colwell and Coddington 1994). We estimated these values using EstimateS 9.1.0 with 50 randomized runs and sampling without replacement (Colwell 2013). We also re-scaled species richness with sample-based rarefaction curves by individuals to adjust for differing densities of sampled individuals (Gotelli and Colwell 2001). Using Ecosim 7.0 (Gotelli and Entsminger 2008), we constructed individual-based rarefaction curves (with 1000 iterations) to calculate expected species richness when we sampled a similar number of individuals from each site. We scaled our estimate of species richness to the lowest number of individuals caught at a site (Mountain View, n=13). We used JMP v 11 to perform the regressions (SAS Institute Inc., Cary, NC).

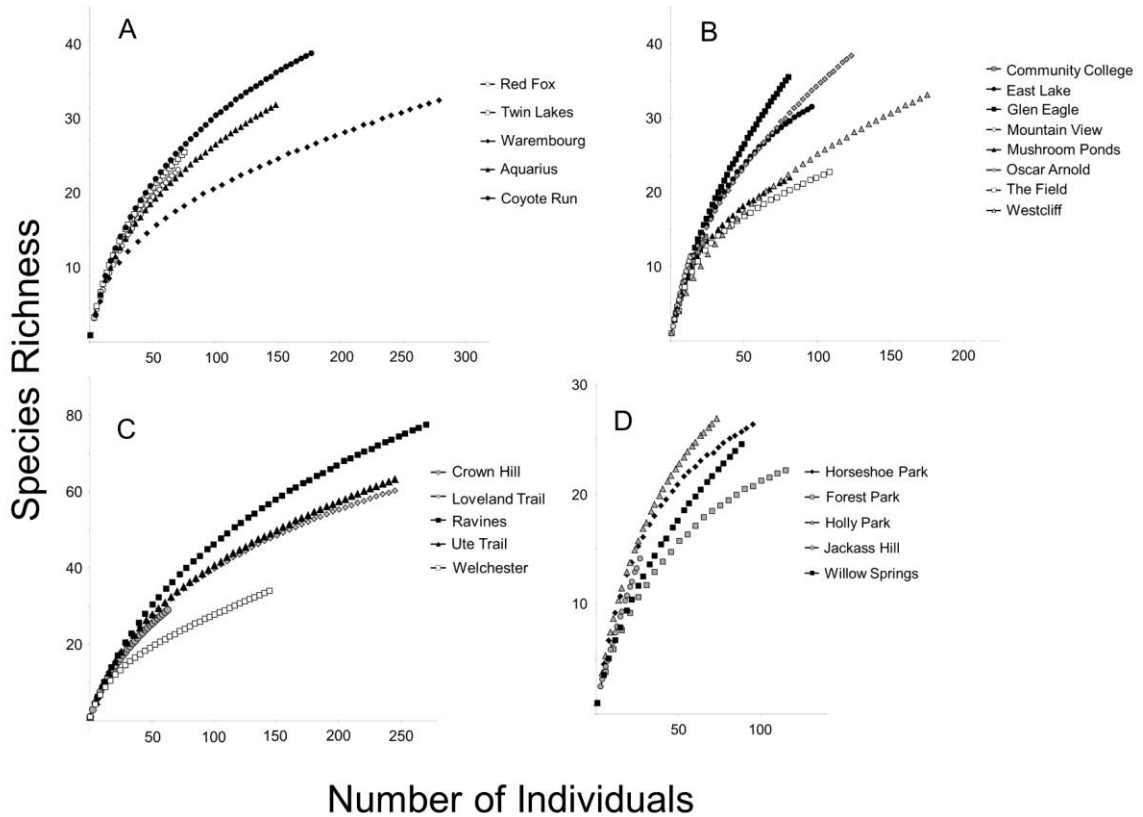
To evaluate whether community composition changed with varying site characteristics, we used redundancy analysis (RDA) to assess the moth composition in sites with varying size, proportion grass, illuminance, and luminance. We used RDA to

constrain our moth communities by these measured environmental factors to determine how well they characterized moth communities. We assessed the significance of the RDA using a permutation test with 999 randomized runs (Legendre and Legendre 2012). As the RDA explained a low percentage of the variability in species composition, we also used the first two unconstrained axes of the model (PC axes); the PC axes correspond with the patterns in species composition unexplained by the measured environmental variables. We used R software (R Development Core Team 2016) to perform the RDA using the package *vegan* (Oksanen et al. 2011).

## Results

We collected 3,107 individual macromoths and identified 185 unique species in the 82 collections from 23 sites. However, as seen in our rarefaction curves (Figure 1) and our estimates of total moth diversity (Appendix Figure B1), there is likely more moth richness in our study system. With this information in mind, we adjusted species richness in two ways. First, we estimated the total number of species expected using three different estimators. Second, we scaled species richness using individual-based rarefaction curves to estimate richness when 13 individuals are randomly sampled. The multiple regression using estimated total species richness was the only significant model ( $F_{4,18} = 3.78$ ,  $p = 0.02$ ). Our multiple regressions using abundance and individual-based adjusted richness were not significant (abundance:  $F_{4,18} = 2.33$ ,  $p = 0.10$ ; richness:  $F_{4,18} = 1.82$ ,  $p = 0.17$ ); however, certain coefficients in the models were significant (Table 1). In all three multiple regressions, there was no relationship between either site size or proportion grass on moth abundance and richness. We did see greater moth abundance

and species richness with increasing illuminance (Table 1). However, increased luminance negatively affected moth abundance and richness (Table 1).



**Figure 1. Individual-based rarefaction curves illustrating the relationship between species richness and the number of individual moths randomly sampled from each fragment in sites in (a) Boulder, (b) Westminster, (c) Lakewood, and (d) Centennial. The figure is divided by area to visualize differences between sites located near each other.**

In our multivariate analyses, illuminance, luminance, and proportion grass were most effective in separating sites (RDA1 6% Figure 2a) with sites in highly populated areas having greater positive scores (e.g. Ute Trail, Loveland Trail, and Ravines). These highly-populated sites had moth species that use as rabbitbrush (*Chrysothamnus viscidiflorus*) as a host plant as larvae, like *Digrammia curvata* and *Schinia albafascia*.

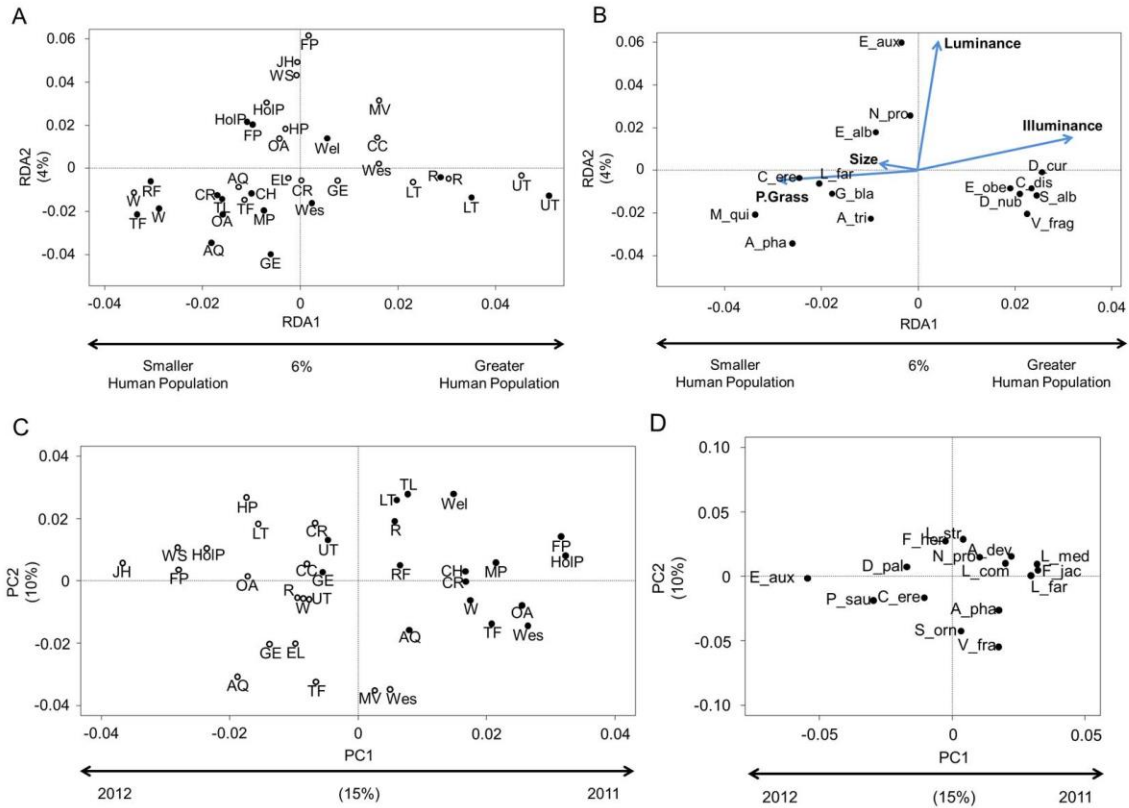
Sites with negative scores (e.g. Warembourg and Red Fox), occurred in less densely populated areas, and had a greater proportion of grass but were also generally darker. These conditions allowed for uncommon species, like *Manduca quinquemaculata* and *Apantesis phalerata* to occur (RDA1 6% Figure 2b).

**Table 1. Multiple regressions of area, proportion grass, illuminance, and luminance on macromoth abundance, individual based estimates of species richness, and estimates of total species richness. All independent variables are independent of each other and are transformed to approach normality of residuals. Bolded coefficients are significant.**

| Dependent Variables                  | Predictor Variables | DF       | F            | p             | Coefficient (SE)         |
|--------------------------------------|---------------------|----------|--------------|---------------|--------------------------|
| Macromoth abundance                  | Area                | 1        | 0.19         | NS            | -16.04 (36.70)           |
|                                      | P. Grass            | 1        | 0.20         | NS            | 34.81 (77.15)            |
|                                      | <b>Illuminance</b>  | <b>1</b> | <b>5.50</b>  | <b>0.0307</b> | <b>124.45 (53.09)</b>    |
|                                      | <b>Luminance</b>    | <b>1</b> | <b>7.93</b>  | <b>0.0115</b> | <b>-2115.26 (751.33)</b> |
| Macromoth species richness           | Area                | 1        | 1.79         | NS            | -0.80 (0.60)             |
|                                      | P. Grass            | 1        | 0.0081       | NS            | -0.11 (1.26)             |
|                                      | <b>Illuminance</b>  | <b>1</b> | <b>5.28</b>  | <b>0.0337</b> | <b>1.99 (0.87)</b>       |
|                                      | <b>Luminance</b>    | <b>1</b> | <b>4.77</b>  | <b>0.0424</b> | <b>- 26.48 (12.26)</b>   |
| Estimated macromoth species richness | Area                | 1        | 0.54         | NS            | -0.07(0.10)              |
|                                      | P.Grass             | 1        | 0.15         | NS            | 0.08(0.20)               |
|                                      | <b>Illuminance</b>  | <b>1</b> | <b>7.09</b>  | <b>0.0158</b> | <b>0.37(0.14)</b>        |
|                                      | <b>Luminance</b>    | <b>1</b> | <b>14.09</b> | <b>0.0015</b> | <b>-7.44(1.98)</b>       |

While the entire RDA model was significant (adjusted  $R^2 = 0.064$ ,  $F = 1.58$ ,  $p = 0.002$ ), the environmental variables we measured only accounted for 6% (RDA1) and 4% (RDA2) of the variation in community composition. Therefore, we analyzed the unexplained variance (PC1 and PC2) to interpret the results further. We found that year of collection explained the first residual axis (PC1 15% Figure 2c,d). Sites visited in 2011 had more positive site scores while those visited in 2012 had more negative scores (Figure 2c). Additionally, year also explained the abundance of *Euxoa auxiliaris*, a

common pest species known as “miller moths”, as 2012 was an outbreak year for this species (Figure 2d).



**Figure 2.** Figure 2 displays (a) RDA site scores (Scaling = 1) for the 23 sites samples throughout the summers of 2011 and 2012 (filled circles = 2011, open circles = 2012), (b) RDA species and environmental parameters scores (Scaling = 1), (c) site scores of the first and second axes of the residuals of the RDA model (PC1 and PC2), (d) species scores of the residuals of the RDA model (PC1 and PC2). We displayed only the centroids (site scores means) of each site (filled circles = 2011, open circles = 2012); site codes are included in Appendix Table B1. We scaled species scores by dividing by 20 and are represented by codes detailed in Appendix Table B2. For simplicity, we show only the 15 species with the highest scores in each figure.

## Discussion

Our results demonstrate that different measures of light pollution can have opposing effects on communities, which has not been suggested in the current literature. Increased illuminance, or the brightness of the source of light, led to an increase in moth abundance and total richness and individual-based estimate of species richness. This



finding is unexpected as we initially predicted that more light pollution from streetlights would decrease abundance and richness. Sources of light pollution near sites and within flight range likely attract moth individuals and more species from nearby communities in the surrounding matrix, and thus increase abundance and richness in the light polluted sites. Our prediction that luminance, or light reflected off an object, would have fewer moth individuals and species, however, is supported. As objects in a site, including moths, become brighter from indirect sources of light (i.e. sky glow), abundance and richness of moths decreases. Thus, our results demonstrate that light pollution from streetlights and other immediate light sources has different impacts on communities than wide ranging, pervasive light pollution across degraded night skies. Many studies of light pollution only consider illuminance to be important (Santos et al. 2010; Rotics, Dayan, and Kronfeld-Schor 2011; Da Silva, Valcu, and Kempenaers 2015; Kamrowski et al. 2014), but our findings suggest that any artificial lighting that affects object visibility, or luminance, also contribute to responses to light pollution. Therefore, it is important for future work to justify whether measures of illuminance, luminance, or both, are important to consider.

We found increased moth abundance and richness in sites with more illuminance, which is evidence for an ecological trap. Our results demonstrate that moths are attracted to sites with high levels of illuminance caused by nearby sources of light, like streetlights. Moths that occur in these brighter areas are subject to higher rates of predation from vertebrate predators like birds and bats (Rydell 1992; Frank 1988). Moths are attracted to artificial light because they use natural light from the moon to orient during flight. Because artificial lights mimic the formerly reliable cue for orientation and attraction to

artificial lights increases predation rate on moths, there is evidence that light pollution induces an ecological trap for moths.

Attraction to illuminated areas may also have consequences that go beyond increased predation to individual moths attracted to bright lights. Surviving moths attracted to areas of high illuminance may continue their lifecycle by mating and ovipositing in these brighter areas. In some habitats, streetlights actually increase the number of ground-dwelling predators (Davies, Bennie, and Gaston 2012) and therefore may increase predation on larvae; however, we found that predation rate under streetlights is not different in our system (Grenis, Tjossem, and Murphy 2015). We are finding that there are other fitness consequences of attraction to streetlights including altering plant-herbivore interactions and competitive interactions among plants (Grenis and Murphy, in prep), as well as physiological impacts (Grenis, Slayter, and Murphy, in prep).

The negative consequences from increased numbers of moths in highly illuminated areas, paired with the decrease in moth abundances and richness from increased luminance, may play an important role in observed declines in worldwide moth abundance and richness (Fox 2013; Conrad et al. 2006). In fact, light pollution is often considered to be a large contributing factor to these decreases but until now, has never been tested. Our study demonstrates that light pollution is indeed a factor that may lead to these widespread declines by both negatively affecting moth abundance and richness directly and inducing an ecological trap.

The results from our multivariate analysis suggest that there is some relationship between vegetation cover and illuminance (Figure 2a,b). Human population abundance

in nearby municipalities may explain this environmental gradient. Sites with more illuminance are located in areas with higher human populations and higher grass cover; in the last census, cities near highly illuminated sites, like Lakewood and Centennial, had 147,214 and 106,114 inhabitants respectively (US Census 2010). Conversely, sites in darker areas, like Gunbarrel and Louisville, have human populations with 9,263 and 19,588 inhabitants respectively (US Census 2010). In their review, Neil and Wu (2006) suggest that urbanization causes shifts in plant phenology that could affect entire communities and higher trophic levels. Our results reflect that possibility as darker sites had higher proportions of grasses, possibly reflecting a more natural ecosystem and brighter sites had higher levels of other herbaceous plants; however, we did not explicitly measure vegetation richness or composition.

Our study also demonstrates interesting patterns unique to locally occurring moth species as well. We found that sites with more illuminance have moth species that use rabbitbrush as a host plant and are commonly distributed west of the Rocky Mountains. Interestingly, we found species with an eastern distribution in sites with more grass but less illuminance, even though few of these species actually consume grasses as a host plant. In fact, the species that consume grasses and might be expected to occur more frequently in grassier sites (i.e. *Noctua pronuba* and *Euxoa auxiliaris*) occurred in sites with the highest luminance. These two species are common and widely distributed across the Great Plains and West; they are also habitat and host-plant generalists (Powell and Opler 2009) suggesting that there are some species that will persist despite changes to their environment, including light pollution.

Our RDA axes only explained 10% of the variation in species composition based on the environmental variables we measured. We thus examined the first two residual PC axes, and found a clear relationship between species composition and year (PC1 15% Figure 2c,d). This suggests that our results should be viewed as highly contextual. We offer some potential explanations for the variation in species composition between years. In Colorado, 2011 was a drier year for Colorado followed by a mild 2012 winter (US Drought Monitor 2016). The drier summer in 2011 extended the flight season of *E. auxiliaris* and the mild winter in 2012 reduced juvenile mortality. These two factors allowed more *E. auxiliaris* to persist in the environment resulting in a heavy ‘miller moth’ season with atypically large numbers of these moths in Colorado. To further support this pattern, we found *E. auxiliaris* at every site sampled in 2012 while only 29% of sites contained this species in 2011. Because moths are sensitive to fluctuations in annual weather conditions, it is not unsurprising that our two collection years had different moth community compositions.

In summary, our study demonstrates that different measures of light pollution can have opposing effects on communities. Increased luminance directly affects abundance and richness of moth communities negatively. Increased illuminance increases moth abundance and richness but has important negative consequences for individuals attracted to lights. Because light pollution has opposing effects on moth communities, there are two ways in which light pollution contributes to worldwide declines in moth communities. Therefore, consideration of both illuminance and luminance are required when studying the impacts of light pollution on species and communities.

**CHAPTER TWO: PREDATION OF LARVAL LEPIDOPTERA IN HABITAT  
FRAGMENTS VARIES SPATIALLY AND TEMPORALLY BUT IS NOT  
AFFECTED BY LIGHT POLLUTION**

**Introduction**

Increased anthropogenic development of native landscapes leads to habitat loss and fragmentation, which may reduce biodiversity and change species interactions (Saunders, Hobbs, and Margules 1991; Fahrig 2003). One of the most pronounced changes in these altered habitats is that of increased edge habitat and its effects on species (Saunders, Hobbs, and Margules 1991; Ries and Sisk 2004; Lindenmayer and Fischer 2006). Changes in the abiotic environment along edges, such as wind, light exposure, and temperature, translate to a wide range of biotic responses (Saunders, Hobbs, and Margules 1991), including changes in ecosystem services, species distributions, and trophic interactions. For example, some smaller predators actively prefer habitat edges, while others require core habitat conditions to persist in the environment (Andren 1994; Didham et al. 1996). Increases in predator presence can translate to higher predation rates for prey living along the edge (Gates and Gysel 1978; Quinn and Harrison 1988; Chalfoun, Thompson, and Ratnaswamy 2002; Ries and Fagan 2003; Batary and Baldi 2004; Wimp et al. 2011). However, the general trend of increased predation rate along edges is based primarily on avian studies and should be applied cautiously to other

systems until more studies on other species confirm its applicability to other systems (Wimp et al. in review).

Contrary to the consistent result of high predation rates along habitat edges in avian studies, empirical studies on arthropod communities have shown positive, negative or no change in invertebrate predation. For example, Bolger et al. (2000) found consistent distributions of species, including predators, between the edge and core, while Ries and Fagan (2003) found higher insect predation rates along habitat edges and Wimp et al. (2011) found declines in specialist predators along the edge but a positive response by generalist predators. Yet even in the insect literature, a bias towards diurnal studies or no distinction between diurnal and nocturnal predation ignores potentially important daily variation in predation and core–edge dynamics that could explain the divergent responses previously measured.

Abiotic conditions experienced by edge and core habitats in the day and night vary, and thus the types and abundances of predators in these habitats may also fluctuate temporally. For example, during the day, edges differ in the amount of solar radiation, wind, moisture, and temperature that they experience compared to core habitat (Saunders, Hobbs, and Margules 1991; Lindenmayer and Fischer 2006). Notably, previous research shows that temperature differences across patches may equalize during the night and provide less microhabitat variation nocturnally between edge and core (Daily and Ehrlich 1996; Ricketts et al. 2001). Variation in abiotic conditions that create microhabitats are important for small invertebrates as even the smallest changes may offer a refuge from environmental changes and predation (Bolger et al. 2000; Schoonhoven, van Loon, and

Dicke 2005; Gibb and Hochuli 2006); overnight, microhabitat differences between the core and edge may dissipate (Daily and Ehrlich 1996; Ricketts 2001). In habitat patches surrounded by urban and suburban development, the types of predators present, predator abundance, and behavior, may also be influenced by the presence of artificial light at night.

Artificial lighting can change predator communities and foraging habits. Visual hunters, such as diurnal shorebirds, for example, are able to extend their foraging periods when areas are lit at night (Santos et al. 2010). Some vertebrate predators, such as birds and bats, forage preferentially under street lights because their prey is attracted to artificial lights (Frank 1988; Rydell 2006) while other nocturnal species, like spiny mice, are photophobic and will avoid foraging in areas where they are also more readily seen by their own predators (Bird, Branch, and Miller 2004; Rotics, Dayan, and Kronfeld-Schor 2011). Invertebrate predators appear to prefer artificially lit areas. In laboratory experiments, orb weaving spiders preferentially build webs in lighted environments (Heiling 1999) and in England, ground dwelling invertebrate predators are present in greater densities under street lights (Davies, Bennie, and Gaston 2012). For insects living along habitat edges, greater densities of invertebrate predators may translate to greater nocturnal predation pressure under streetlights not only due to predator preference for foraging along edges (Bolger et al. 2000; Ries and Fagan 2003; Davies, Bennie, and Gaston 2012), but also because of variation in illumination along the edge. Whether street lighting affects predation rates of ground-dwelling prey, like larval Lepidoptera, however, has not yet been tested.

In this study, we examine whether predation rates on ground-dwelling invertebrate larvae by vertebrate and invertebrate predators vary spatially and temporally in urban habitat fragments. We test the hypothesis that predation rate of larval Lepidoptera differs between edge and core habitats and also that predation along the habitat edge varies in response to light pollution from streetlights. We also test whether predation rate varies temporally between day and night. Because there are stark differences in abiotic conditions affecting predator distributions diurnally, we expect that predation rate in edge habitats will be higher than in core habitats during the day, but the difference in predation rate may disappear at night. Additionally, we examine whether the presence of artificial lighting influences predation rate. As light pollution has been shown to alter predator communities, we expect that predation rates should vary with the presence of artificial lighting, and that predation will be greatest under streetlights where predator density is likely to be highest.

## **Methods and Materials**

### **Study Sites**

The Denver-Metro area has many Open Space programs devoted to preserving and restoring native ecosystems along the Eastern Foothills of the Colorado Rocky Mountains. Open Spaces generally consist of patches of mixed grass prairie with a number of both native and exotic species of forbs and grasses; trees and other woody vegetation are limited to small riparian drainages (Nufio, McClenahan, and Bowers 2010b; Hinnert, Kearns, and Wessman 2012). These patches are unique in that they are



“islands” of natural prairie habitat in an otherwise residentially-developed landscape, but they are able to maintain a diverse community of insects including bees, butterflies, grasshoppers, and moths (Nufio, McClenahan, and Bowers 2010; Hinners, Kearns, and Wessman 2012; Robinson, Armstead, and Bowers 2012, Grenis and Murphy unpublished data). For this study, we selected 8 prairie sites between 5 and 15 ha in size with 2–5 street lights along the edge of the habitat patch. Sites were located throughout the Front Range in the City and County of Broomfield, the City of Lakewood, the City of Louisville, and the South Suburban Parks and Recreation District (Appendix Table B3).

### Experimental Design

For our study, we used wax worm (*Galleria mellonella* Linnaeus) larvae as prey because they have minimal defenses and are readily consumed by generalist invertebrate predators (K. Grenis and B. Tjossem, personal observation). We obtained larvae for each experimental trial from pet stores in the Denver Metro area as wax worm larvae are commonly fed to insectivorous pets. We pinned each wax worm larva to a square of Styrofoam (10 cm x 10 cm x 1.5 cm) with a 00 size insect pin through one of the last two abdominal segments (methods adapted from Frank and Shrewsbury 2004). Prior to deploying larvae in the field, we conducted a pilot experiment in the laboratory to ensure that pinned larvae would remain alive for at least 24 h and also not be able to escape, thus ensuring that disappearances in the field would be due solely to predation. We found that none of the 30 wax worms pinned in the lab died or escaped after 24 h, which is the maximum amount of time a larva would spend in the field. Therefore, we reasonably

assume that any wax worm disappearances in the field were caused by some predation event rather than by escape.

## Field Experiment

For each trial during our field experiment, we placed 15 individually-pinned wax worms at each site in one of three habitat treatments: 5 in the core of the patch (at least 30m from edge), 5 along the edge under streetlights, and 5 along the edge at least 10m from a streetlight. There was some variation in the number of larvae deployed among sites because not all sites had 5 streetlights (see Appendix Table B3). We placed individual larvae in the experimental treatments across the entire field site; for example, larvae in the unlit edge treatment were dispersed along multiple parts of the unlit edge and were not grouped together. The wax worm larvae placed along the patch edge were at least 1 m from the edge (usually a street or sidewalk) but no more than 4 m into the patch. Our method measures the maximum predation rate within each habitat treatment (non-experimental larvae may conceal themselves or modify their behaviors to avoid predation) and thus allows us to compare predation rates among treatments, but is not a measure of natural predation rate on unpinned larvae.

To investigate diurnal predation, we deployed wax worm larvae at dawn (~06:00; we adjusted the times for deployment and recovery throughout the season as day length lengthened and then shortened) using the Styrofoam square described above and nailing the square to the ground with a large 15 cm nail. We pinned only one wax worm larva to each Styrofoam square. We labeled the Styrofoam squares with a “please do not

disturb’’ tag with information about the experiment to avoid manipulation from curious visitors. To facilitate recovery of wax worm larvae in the core where visible landmarks were scarce, we placed a surveyor’s flag at least 3 m away from the Styrofoam square in a haphazardly chosen cardinal direction (N, S, E, or W) to ensure that predators would not associate the marker with food. After pinning each larva to its own Styrofoam square, we used calipers to measure body length (to the nearest 0.01 mm). We returned to each site at dusk (~19:00), and recorded the status of the wax worm (predated or not predated). Wax worm larvae were considered predated if they were completely missing, half gone, or showed evidence of predation such as necrotic tissue around an open wound. During our dusk and dawn collections, we also took note of any predators that we found feeding on the wax worm. Additionally, during the early July observation period, we spent 5 h (09:00–14:00) in three field sites observing predation events to learn predator identities. To examine nocturnal and streetlight predation, we replaced any wax worm larvae that had died during the day (either by predation or desiccation) at dusk (~19:00) and recorded the status of the wax worm (predated or not predated) the following morning at dawn (~06:00).

We repeated this entire experimental design twice per month (e.g. early June and late June) in June, July and August, 2013. Thus, we had a total of six collection periods, which allowed us to account for the appearance and emergence of various predators during the summer, and our sampling periods were temporally separated to prevent learning by predators. All eight sites were used in each trial except the nights of the

second and sixth sampling periods because of inclement weather (Late June, n = 7 sites; Late August, n = 6 sites).

### Statistical Analyses

We used multiple logistic regressions to test our hypotheses. First, we examined whether predation rates varied between the day and night using a logistic regression with predation (binomial response: 1 for predated, 0 for alive) as the dependent variable and larval body *length* as the continuous independent variable. Our categorical independent variables were *site*, *sampling period* (early June, late June etc.), *time of day* (day or night), and the interaction effect of *sampling x period time of day*. Our model showed no evidence of overdispersion, so we continued to use *site* as a fixed effect, even though it was not a variable of particular interest for our primary research questions (Warton and Hui 2011).

For our analyses of how unlit core and unlit edge habitats differ in predation rate over time, we excluded larvae from the streetlight treatment in order to compare unlit core with unlit edge. We analyzed whether a larva was predated (binomial response: 1 or 0) using a logistic regression with larval body *length* as a continuous covariate and *site*, *sampling period*, *patch location* (core or edge), and the interaction effect of *sampling period x patch location* as categorical fixed effects.

For our analyses of how street-lit and unlit edge habitats differ in predation rate, we excluded larvae from the unlit core treatment. Again, we analyzed whether a larva was predated (binomial response: 1 or 0) using a logistic regression with larval body

*length* as a continuous covariate and *site*, *sampling period*, *patch location* (lit or unlit edge), and the interaction effect of *sampling period x patch location* as categorical fixed effects. In all of our tests, we dropped the interaction effect from the final model if it was not significant. We used JMP v 10.0.0 for all analyses (SAS Institute Inc., Cary, NC).

## Results

Over the course of the summer, we deployed 1,366 wax worm larvae and 56 % of those larvae were predated. The most common observed predators were ants, during both diurnal and nocturnal time periods; of 761 observed predation events, 309 (40 %) were due to ants. Other predators that we observed included wolf spiders and wasps; wasps systematically divided and removed larvae in pieces from the Styrofoam platform. Scavengers, like earwigs, were found feeding on or near larvae after death. Birds are major predators of lepidopteran larvae in many systems, but we never observed them eating larvae during our experiments. Of our 141 trials, only 2% (n = 4) had all of the larvae eaten in a single treatment at a site suggesting that it was not common for a single predator to follow the patch edge and consume all of the larvae.

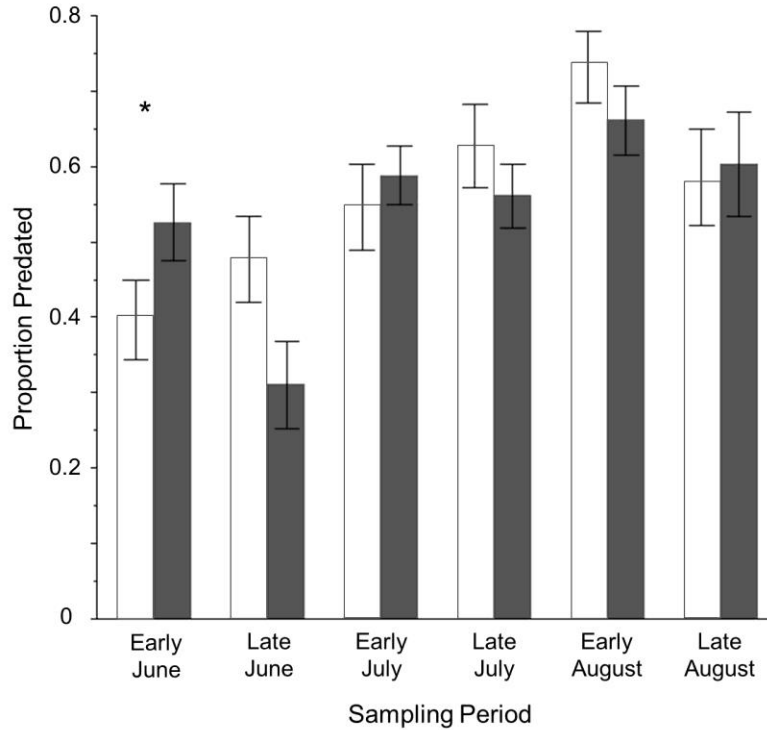
### Predation rate between day and night

When all habitat types are analyzed together, we found that there were no differences in predation rate during the day and night but there was an interaction between *sampling period* and *time of day* because predation rate was higher at night than during the day, but only during the first sampling period (Table 2; Figure 3).

Additionally, predation rate varied by field site, driven primarily by high levels of predation in two field sites (Coyote Run and Jackass Hill) and low levels of overall predation at another field site (The Field 1), but showed no discernable spatial patterns to explain the differences in predation rate (i.e. the high predation sites were not close to each other; Appendix Figure B2). Finally, larval body *length* had no effect on whether larvae were predated in any of our analyses (Table 2).

**Table 2. Logistic regression results from five tests. Bolded values are significant. If an interaction was not significant, it was dropped from the model and not reported.**

| Test                                    | Predictor Variables                  | DF             | $\chi^2$     | p                 |
|---|--------------------------------------|----------------|--------------|-------------------|
| Day-Night                               | Time of Day                          | 1              | 1.29         | 0.26              |
|   | <b>Sampling Period</b>               | <b>5</b>       | <b>46.87</b> | <b>&lt;0.0001</b> |
|   | <b>Time of Day x Sampling Period</b> | <b>5</b>       | <b>18.17</b> | <b>0.003</b>      |
|   | <b>Site</b>                          | <b>7</b>       | <b>61.96</b> | <b>&lt;0.0001</b> |
|   | Length                               | 1              | 1.75         | 0.2               |
| Day: Core vs. Edge                      | <b>Patch Location</b>                | <b>1</b>       | <b>5.40</b>  | <b>0.02</b>       |
|   | <b>Sampling Period</b>               | <b>5</b>       | <b>20.52</b> | <b>0.001</b>      |
|   | <b>Site</b>                          | <b>7</b>       | <b>49.4</b>  | <b>&lt;0.0001</b> |
|   | Length                               | 1              | 0.71         | 0.4               |
|   | Night: Core vs. Edge                 | Patch Location | 1            | 3.35              |
| <b>Sampling Period</b>                  |                                      | <b>5</b>       | <b>25.45</b> | <b>&lt;0.0001</b> |
| <b>Patch Location x Sampling Period</b> |                                      | <b>5</b>       | <b>12.78</b> | <b>0.03</b>       |
| <b>Site</b>                             |                                      | <b>7</b>       | <b>34.15</b> | <b>&lt;0.0001</b> |
| Length                                  |                                      | 1              | 0.068        | 0.8               |
| Day: Unlit vs. Lit                      | Patch Location                       | 1              | 0.004        | 0.9               |
|   | <b>Sampling Period</b>               | <b>5</b>       | <b>19.35</b> | <b>0.002</b>      |
|   | <b>Site</b>                          | <b>7</b>       | <b>31.24</b> | <b>&lt;0.0001</b> |
|   | Length                               | 1              | 0.06         | 0.8               |
|   | Night: Unlit vs. Lit                 | Patch Location | 1            | 0.02              |
| <b>Sampling Period</b>                  |                                      | <b>5</b>       | <b>15.19</b> | <b>0.01</b>       |
| <b>Site</b>                             |                                      | <b>7</b>       | <b>14.15</b> | <b>0.05</b>       |
| Length                                  |                                      | 1              | 0.16         | 0.9               |

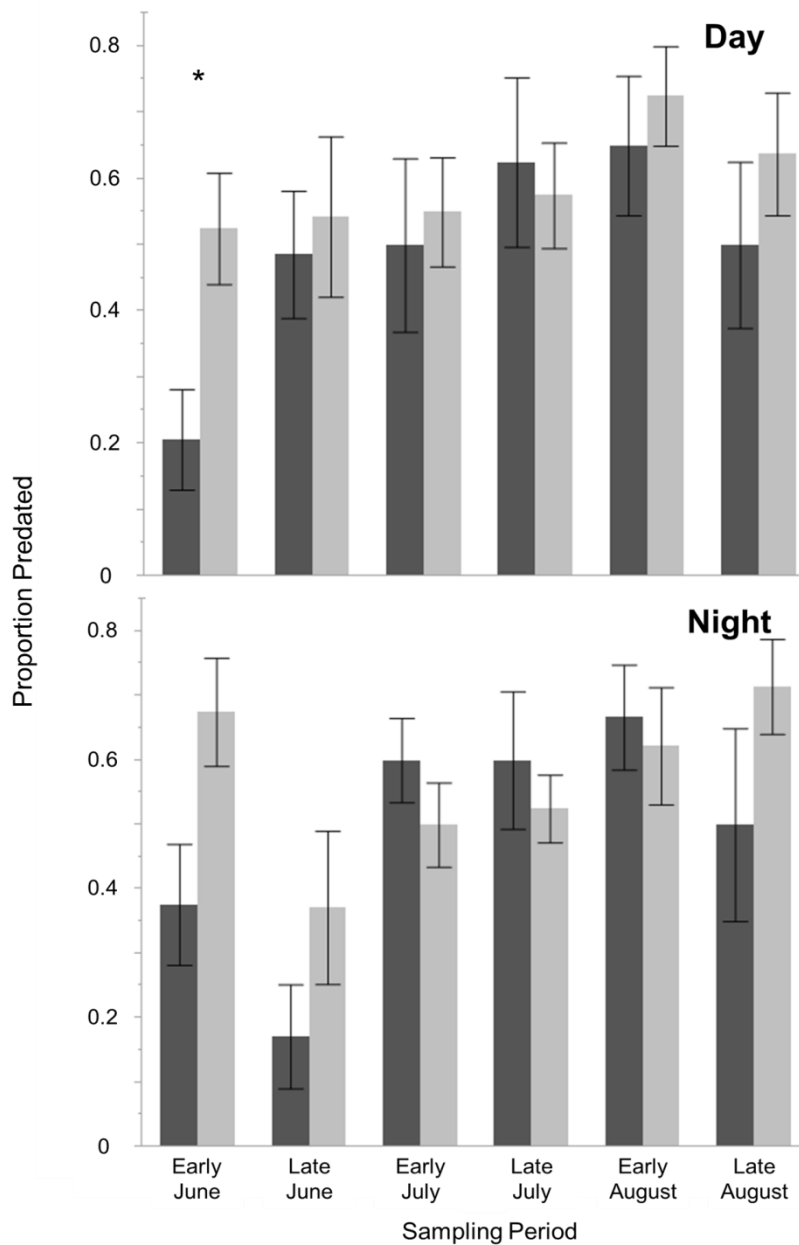


**Figure 3. Proportion of individual larvae (mean  $\pm$ 1 SE) predated during the day (white bars) and the night (black bars) over the course of the summer of 2013. Asterisks denote significant differences in proportion of larvae predated between the day and night during a particular sampling period ( $P < 0.05$  with a Bonferroni correction).**

#### Predation rate in habitat core vs. habitat edge

During the day, larval predation rate was 20% greater along the patch edge compared to the core (Table 2; Figure 4). Predation of larvae increased over the course of the summer in both edge and core habitats (Table 2; Figure 4). Again, field *site* was a significant factor with similar patterns as those detailed above (Appendix Figure B3). During the night, larval predation did not differ between the habitat core and edge but did increase throughout the summer (Table 2; Figure 4); however, there was an interaction between habitat *patch location* and *sampling period* (Table 2). We attribute this

interaction to particularly low predation in the habitat core from inclement weather in late June. Predation rate differed among field sites at night (Appendix Figure B4).

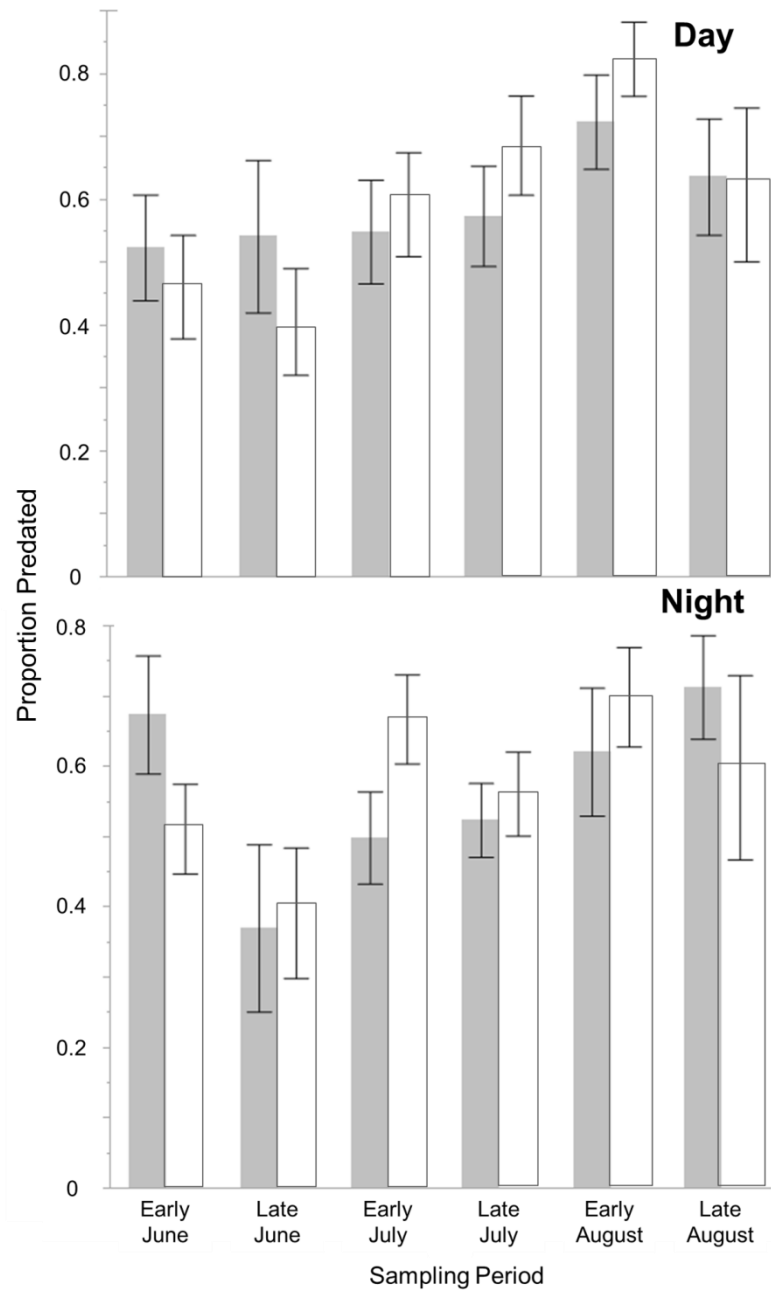


**Figure 4. Proportion of individual larvae (mean  $\pm$ 1 SE) predated along the habitat edge (black bars) and in the habitat core (gray bars) during the day and night over the course of the summer of 2013. Asterisks denote significant differences in proportion of larvae predated between edge and core habitat types during a particular sampling period ( $P < 0.05$  with a Bonferroni correction).**



## Predation rate along unlit edge vs. streetlit edge

We found no differences in larval predation between unlit and streetlit edges during the day but found that, in general, diurnal predation rate increased during the course of the summer in both types of edge habitat (Table 2; Figure 5). Similar to our results during the day, at night we also found no influence of nocturnal streetlighting on larval predation and there was an increase in predation over the summer (Table 2; Figure 5). Predation rate again differed among field sites during the day (Appendix Figure B5) and night (Appendix Figure B6).



**Figure 5. Proportion of individual larvae (mean  $\pm 1$  SE) predated along the habitat edge in unlit areas (black bars) and under streetlights (white bars) during the day and night over the course of the summer of 2013.**

## Discussion

Our results show that predation is significantly greater along habitat edges than in the habitat core, but only during the day. Notably, we found that nocturnal predation rates along the habitat edge are not affected by the presence of streetlights, which indicates that light pollution does not affect the strength of top-down pressures on lepidopteran larvae in fragments of mixed grass prairie surrounded by urban development. Furthermore, although predation rates increased throughout the summer in both habitat types, the greatest difference between edge and core habitats in predation risk for larvae occurred in early June. Thus, the generally accepted idea that edges are dangerous places for prey may instead be a pattern that is restricted to certain times of day and season.

We predicted that changes in predation rate associated with edge and core habitats would have consequences for their prey by increasing predation rate along the edge and these negative effects would vary temporally between day and night. We found that predation rates are higher along the edge as compared to the core, but only during the day, which may help explain why certain species are more sensitive to habitat fragmentation (Lindenmayer and Fischer 2006) and have varying responses to edges (Ries and Sisk 2004). Diurnal insects like butterflies, grasshoppers, and bees generally lose individuals and species richness as habitat sizes shrink and edge effects become more prominent (Hinners, Kearns, and Wessman 2012; Robinson, Armstead, and Bowers 2012; Nufio, McClenahan, and Thurston 2009). However, organisms that are primarily nocturnal, like moths, do not respond negatively to habitat fragmentation and instead

their species richness and abundance shows no discernable pattern with regard to habitat fragmentation (Ricketts et al. 2001; Schmidt and Roland 2006; Fuentes-Montemayor et al. 2012). We found diel fluctuations in edge and core predation rates, with predation greater in edge habitats than core habitats only during the day. Given that foraging and feeding are dangerous activities and expose herbivorous larvae to greater predation risk (Bernays 1997), lepidopteran species with larvae active during the day may be more negatively affected by predation in edge habitats than larvae active at night. Most studies of how Lepidoptera species respond to edges have focused on the adult stages (Fuentes-Montemayor et al. 2012; Ricketts 2001; Summerville and Crist 2004; Schmidt and Roland 2006; Robinson, Armstead, and Bowers 2012), but our research demonstrates that predation risk for the larval stage is also greatly affected by edges and may vary seasonally. Thus, how edges affect different ontogenetic stages needs further investigation as it may help to explain why butterflies and moths have such divergent responses to habitat fragmentation.

We found that light pollution from adjacent streetlights did not alter predation rates, which is surprising as light pollution has greatly altered the night time environment (Cinzano, Falchi, and Elvidge 2001; Kyba et al. 2011) and has been shown to be an important effect in other studies (Bird, Branch, and Miller 2004; Tuxbury and Salmon 2005; Kriska et al. 2009; Santos et al. 2010). On moonless, cloudless nights, patch edges near streetlights can receive light levels up to four times brighter than found during a full moon (Rich and Longcore 2006). Although we expected this change in nocturnal lighting regime to increase predation, our data show that the story might not be as simple.

Research on predators demonstrates that some species are attracted to nocturnal artificial lighting while others respond negatively by avoiding lights or decreasing foraging time in lit areas (Heiling 1999; Bird, Branch, and Miller 2004; Santos et al. 2010; Davies, Bennie, and Gaston 2012). If predator foraging behavior has an additive effect on larval predation, we may find no net effect of street lights on predation risk for larvae despite significant positive and negative effects on different predator species' behavior and abundance. To further understand the impacts of light pollution on herbivores, we need more studies on the behavioral responses of predators to light pollution. Although light pollution likely has important impacts on the functional and numeric responses of predators, our results suggest that artificial lighting may not alter overall predation rates on herbivorous larvae if the positive and negative effects of predation risk are evenly balanced.

We also found that predation increases throughout the summer, which may be due to accumulation in invertebrate predator individuals and species that emerge throughout the summer. Additionally, we may have observed a higher predation rate on our experimental larvae later in the summer if alternate prey decreased in abundance later in the growing season, but we did not measure alternate prey resources. Anecdotally, we noticed changes in vegetation structure throughout the summer that may make prey more visible. In early summer, vegetation in the prairie habitat fragments was lush, thick, and dense, and this vegetation complexity may provide hiding places for prey and obstacles for invertebrate predators. As the season became progressively drier, vegetation thinned and wilted, reducing the vegetation complexity, which may have made it easier for

predators to find prey, but we did not specifically test this. Because predation rate in our study changed so drastically between the early and late summer, our results emphasize the importance of experimental repetition as patterns may vary not only year to year, but within a season as well.

Our data show that predation may be a cause of variation between nocturnal and diurnal invertebrate responses to habitat fragmentation. Because larvae are subject to greater rates of predation while feeding (Bernays 1997), larvae active during the day may be subject to more predation along habitat edges. We suggest that species with diurnal larvae in fragmented landscapes will suffer the effects of habitat fragmentation more than nocturnal species. Additionally, prairie species emerging later in the summer are also subject to greater predation. Our study suggests that late-season invertebrate larvae that are diurnal and live along the edge of a habitat patch will suffer the greatest amounts of predation and therefore will suffer the most from increased habitat fragmentation and subsequent increases in edge habitat, but this prediction needs to be tested in other natural and managed ecosystems accounting for prey evasion of predators.

## **CHAPTER THREE: LIGHT POLLUTION AFFECTS INVASIVE AND NATIVE PLANT TRAITS IMPORTANT TO HERBIVOROUS INSECTS**

### **Introduction**

More than half of the world's population lives in urban or suburban areas (McIntyre et al. 2001) and the associated development has caused nearly 20% of the Earth's night skies to be affected by anthropogenic light (Cinzano, Falchi, and Elvidge 2001; Kyba et al. 2011). Humans light the night to increase nighttime activity, promote safety, and deter criminal behavior (Painter 1996), but frequent exposure to long periods of uninterrupted light has negative impacts not only on humans, but also on adjacent natural communities (Longcore and Rich 2004). Some species, for example, require the dark to forage successfully (Rotics, Dayan, and Kronfeld-Schor 2011) while others use naturally-occurring light, like the moon, as a cue for key behaviors like finding appropriate habitat or orientation during flight (Tuxbury and Salmon 2005; Kriska et al. 2009; Frank 1988). Although light pollution is relatively well-studied for some vertebrates, such as bats, birds, turtles and humans (Rydell 1992, 2006; Rich and Longcore 2006; Navara and Nelson 2007; Santos et al. 2010; Jung and Kalko 2010; Kempenaers et al. 2010; Falchi et al. 2011; Bedrosian and Nelson 2013; Davies et al. 2013; Gaston et al. 2013; Kamrowski et al. 2014; Da Silva et al. 2015; Hale et al. 2015 and references therein), the impacts of artificial lighting have been explored for few

invertebrate systems (Rich and Longcore 2006; but see Davies et al. 2012, 2013; Bennie et al. 2015) and not at all for plant communities that are surrounded by urban areas (Neil and Wu 2006). Furthermore, most studies of light pollution focus on individual species and lack a community perspective (Gaston, Visser, and Hölker 2015). Recently there have been several calls in the literature for studies that investigate how the effects of light pollution vary among species, especially plants and non-vertebrate animals for which we know relatively little, and associated effects on populations, communities, ecosystems, species interactions and ecosystem services (Gaston, Visser, and Hölker 2015; Hölker et al. 2010; Lyytimäki 2013; Gaston et al. 2013; Macgregor et al. 2014). If light pollution has significant effects on individual species, it follows that it may have important implications for community dynamics by altering species interactions, such as between native and invasive species.

Plants exposed to light pollution at night may perform differently than conspecifics under ambient conditions because day length and photoperiod are important signals for plants. Under natural conditions, many plants are cued by day-length to germinate, grow, reproduce, and senesce (Raven, Evert, and Eichhorn 1986) and for some sensitive species, any disturbance in lighting regime may prevent individuals from progressing into different life stages (Neil and Wu 2006; Raven, Evert, and Eichhorn 1986). For instance, one study done in urban systems found that trees planted near street lights delay or stop leaf abscission compared to individuals not near artificial lights (Matzke 1936) and another study found that a leguminous plant produced fewer flower heads when exposed to artificial lights (Bennie et al. 2015). Yet most of the literature on



how continuous photoperiods affect plants only considers agricultural and horticultural systems (Harvey 1922; Neil and Wu 2006; Briggs 2006) and rarely focus on native species. It is unknown if light pollution from streetlights changes plant traits in natural communities that may alter competitive interactions or that are important to herbivores. Notably, whether consumers are directly or indirectly affected by artificial night lighting has never been tested.

Light pollution may act as a disturbance that changes competitive dynamics among invasive and native species. There are dozens of hypotheses that attempt to explain the success of invasive species (Catford, Jansson, and Nilsson 2009); common mechanisms proposed are trait differences between invasive and exotic species (Rejmánek and Richardson 1996), enemy release (Keane and Crawley 2002), and disturbances related to global change, such as habitat fragmentation and climate change (Dukes and Mooney 1999). Of these, only global change considers the role humans may play in promoting invasion of exotic species. For example, exotic species may become invasive due to human-induced changes to the environment, such as habitat disturbances, changes to nitrogen and carbon cycles, climate change, and habitat fragmentation (Dukes and Mooney 1999). To date, no study investigates whether light pollution could be a contributing anthropogenic disturbance that promotes invasive plant colonization and growth.

In this study, using a series of laboratory and field experiments, we test the hypothesis that light pollution affects plant traits important to fitness and impacts higher trophic levels indirectly through plant-mediated changes. In particular, we predict that

exposure to consistent low levels of light at night may affect plant traits, such as germination rates, biomass and nutrient content, and we explore whether these effects differ between invasive and native grass species. We also examine whether herbivore growth and survival are indirectly affected by the development of their host plant under artificial night light or whether these traits are directly affected by exposure of the herbivore to artificial light during development.

## **Materials and Methods**

### **Study System**

The Denver-Metro area has many Open Space programs devoted to preserving and restoring native ecosystems along the Eastern Foothills of the Colorado Rocky Mountains. Open Spaces generally consist of patches of mixed grass prairie with a number of both native and invasive species of forbs and grasses; trees and other woody vegetation are limited to small riparian drainages (Hinners, Kearns, and Wessman 2012; Nufio, McClenahan, and Bowers 2010). These patches are “islands” of natural prairie habitat in an otherwise residentially-developed landscape, but they maintain a diverse community of insects including bees, butterflies, grasshoppers, and moths (Nufio, McClenahan 2010; Hinners, Kearns, and Wessman 2012; Robinson, Armstead, and Bowers 2012). For the field component of our study, we selected eight prairie sites between 5 and 15 ha in size with 2-5 streetlights along the edge of the habitat patch (Appendix Table B3).

## Plant Performance - Greenhouse

To investigate the effects of light pollution on common prairie grasses, we initiated a greenhouse experiment in the early summer of 2013 to test effects of nocturnal artificial lighting on germination, aboveground and belowground biomass, and nutrient content (C:N ratio) of six common prairie grasses. We selected six species commonly found in prairie fragments throughout the Denver-metro area. We planted four grass species native to shortgrass prairies: alkali sacaton (*Sporobolus airoides* Torr.), buffalo grass (*Buchloe dactyloides* Nutt.), blue grama (*Bouteloua gracilis* [H.B.K.] Lag.), and western wheatgrass (*Agropyron smithii* Rydb.). We also planted two common invasive species introduced for livestock grazing and erosion prevention: cheatgrass (*Bromus tectorum* L.) and smooth brome (*Bromus inermis* Leyss.) (EDDMapS 2015).

For each of the six plant species, we placed 10 seeds in each of 60 515cm<sup>3</sup> cone-tainers (for a total of 360 cone-tainers) filled with garden soil (Miracle Grow Garden Soil; The Scotts Company, LLC.). We evenly distributed the six species into flats, each with 24 cone-tainers, and randomly distributed species within each flat. We then placed half of the flats (180 cone-tainers) into a partitioned greenhouse lit overhead by high-pressure sodium lamps timed to go on at 21:00 and turn off at 06:00, mirroring average length of summer streetlight illumination. Modern streetlights are the same type of high-pressure sodium lamp that we used in our greenhouse and these lights provide light in the 400 to 700 nm spectrum (Longcore and Rich 2004; Cinzano, Falchi, and Elvidge 2001; Frank 1988). We also measured the illuminance of the greenhouse grow lights at 5.5 lux that is less than the amount of illumination of a lit parking lot (Longcore and Rich 2004).

We placed the other half of the flats in a room set to the same temperature and humidity settings but only received natural light as a control group.

We watered all plants with approximately 70mL of water every other day. We rotated flats within each light treatment every week to minimize effects from greenhouse location. Every three weeks, we fertilized plants with 10mL of a 2L dilution of 1%NPK solution to ensure that plants were not nutrient limited. Additionally, every three weeks, we haphazardly rotated individual cone-tainers among flats to decrease within flat and neighbor shading effects.

We monitored germination rate of seeds after one month. We define germination rate as the proportion of ten seeds per cone-tainer that produced seedlings. Based on their germination rates, to equalize potential competition among seedlings we reduced the number of seedlings per cone-tainer and transplanted any excess seedlings into new cone-tainers. We placed five individuals of smooth brome and blue grama, four of cheatgrass, and three of western wheatgrass into each cone-tainer; alkali sacaton and buffalo grass had low germination and did not need to be thinned. We began harvests after each species had sufficient biomass in each cone-tainer for all plant measurements (smooth brome at week 10, blue grama at week 11, cheatgrass and western wheatgrass at week 25; these start dates for harvest varied due to each species' germination time). Every three weeks, we randomly selected five cone-tainers from each species and light treatment to harvest, resulting in six harvests (harvests occurred over a total of 18 weeks). Alkali sacaton and buffalo grass had low germination and growth throughout the experiment so we harvested them only at the end of the experiment (week 43).

After each harvest, we quantified leaf toughness, aboveground dry biomass, belowground dry biomass, and C:N ratio by pooling all individuals within a cone-tainer. We measured plant toughness of the first green blade of grass per culm using the cup-string method detailed in Hendricks et al. (2011); this method tests toughness using the amount of sand required to pull a safety pin through a blade of grass. We measured toughness of each individual plant in each cone-tainer. After we measured leaf toughness, we placed above- and belowground tissues of a given cone-tainer in a drying oven at 60°C for three days to measure dry tissue biomass. To measure treatment effects on C:N ratio, we ground the aboveground biomass in a mixer mill (Retsch MM400) and sent processed samples to the Cornell Stable Isotope Laboratory for nutrient analysis.

#### Plant Performance - Field

To determine whether streetlights affect plant traits in the field, we focused on smooth brome as it was the only species found reliably at all eight field sites. Within each of the eight field sites (Appendix Table B3), we haphazardly selected five streetlit locations and five unilluminated edge locations for plant collection; the unilluminated edge locations were paired with streetlit locations so that the two treatments were interspersed within each site and not clumped. We confirmed that each edge site was illuminated and unilluminated at night in a previous experiment (Grenis, Tjossem, and Murphy 2015). At each location (streetlit or unilluminated), we collected five culms of grass from within a ~5m radius of the streetlight or five culms of grass from the unilluminated edge for a total of 400 culms collected (8 sites x 2 treatments [lit vs.

unilluminated] x 5 locations/treatment x 5 culms/location). In the laboratory, we washed the plants, pooled them by location and then measured leaf toughness, aboveground dry biomass and C:N ratio (see above for methods).

### Herbivore Performance

In late June of 2014, we collected early instar *Apamea sordens* Guenée larvae from our field sites (Appendix Table B3) using sweep nets under streetlights and along unilluminated edges. The *A. sordens* are climbing cutworms and feed on both smooth brome seed heads and leaves. We identified the larvae using COI (cytochrome oxidase I) sequences isolated using LepF1 and LepR1 primers; we sent samples to Eurofins Scientific for sequencing and matched sequences to *A. sordens* using BLAST and BOLD. This species has a high rate of barcode consistency across wide geographic areas (Zahiri et al. 2014).

We brought the larvae back to the laboratory and kept them in individual 0.5L deli containers for immediate use in our greenhouse experiment. We designed a complete factorial experiment to test both the direct and plant-mediated indirect effects of streetlights on larval fitness. To test the indirect effects of streetlights on larval fitness mediated by host plant effects, we reared larvae on smooth brome that corresponded to the plants where we had collected the larvae from the field: plants collected from under streetlights in the field or plants collected from along the unilluminated edge. We continued to feed them the host plant on which we found them because we were not interested in looking at host-switching effects in this experiment. We fed each larva its

corresponding host plant *ad libitum* once per week by replacing the old plant material in each deli container with freshly collected plant material. To test the direct effects of artificial lighting on larval fitness, we placed half of the larvae feeding on each type of host plant (streetlit or unilluminated) into the greenhouse under high-pressure sodium lamps that illuminated them from 21:00 until 06:00, mirroring average streetlight duration during the summer, and we placed the other half of the larvae from each host plant treatment into control (ambient) conditions with normal day-night cycles (4 plant/lighting treatments ~ 20 larvae/treatment = 82 larvae total). During feedings, we monitored survival and removed any frass. Additionally, we measured body mass of ten randomly selected larvae from each treatment at the beginning of the experiment and every following week for 10 weeks to measure accumulated body mass. At the end of the summer, we measured final body mass of all larvae.

### Statistical Analyses

To determine if plant species responded differently to artificial lights, we used a two-way ANOVA with *treatment*, *species*, and *treatment x species* interaction as the independent variables; germination, aboveground biomass, aboveground-belowground biomass ratio, C:N ratio, and toughness were our dependent variables. We divided the cone-tainer mean of aboveground biomass and toughness by the number of seedlings in a cone-tainer as there was varying numbers of individuals in each cone-tainer due to low germination or seedling death. When appropriate, we used a log transformation to get

dependent variables aboveground-belowground biomass ratio, toughness, and C:N ratio to conform to the assumption of normality.

To determine whether plant traits are differentially affected by streetlights over time, for the species we harvested every three weeks, we used four ANOVAs to test the effect of artificial lights on the dependent variables: aboveground biomass, aboveground-belowground biomass ratio, toughness, and C:N ratio. When appropriate, we used a log or root transformation to get dependent variables to conform to the assumption of normality. Our independent variables were *treatment*, *harvest*, and *treatment x harvest* interaction.

To determine whether streetlights affect smooth brome plants in the field, we used a two-way ANOVA with *patch location* (streetlight edge or unilluminated edge), *field site*, and the *patch location x field site* interaction as independent variables. We kept field site as a fixed effect because of our small number of field sites (Warton and Hui 2011). We used aboveground biomass, toughness, and C:N ratio as the dependent variables.

We analyzed data from the larval performance study using Kaplan-Meier survival curves for each of the four plant/lighting treatment combinations. We also used two-way repeated measures ANOVAs with *light treatment*, *host plant*, and the *light treatment x host plant* interaction as the independent variables with growth rate and mass of the 40 weekly-monitored larvae as continuous dependent variables. These data violated the assumption of sphericity (growth rate:  $\chi^2 = 93.11$ ,  $df = 35$ ,  $p < 0.0001$ , mass:  $\chi^2 = 178.6$ ,  $df = 44$ ,  $p < 0.0001$ ) so we used a repeated measures MANOVA with a Greenhouse-Geisser degrees of freedom correction for these analyses (growth rate:  $\epsilon = 0.50$ , mass:  $\epsilon =$



0.27). To determine at which time points treatments differed, we used two-way ANOVAs at each time point with a Bonferroni correction. Additionally, to evaluate performance of larvae at the end of the experiment, we used a two-way ANOVA with *light treatment*, *host plant*, and the *light treatment x host plant* interaction as independent variables and final body mass as the continuous dependent variable. We used JMP v 11 for all analyses (SAS Institute Inc., Cary, NC).

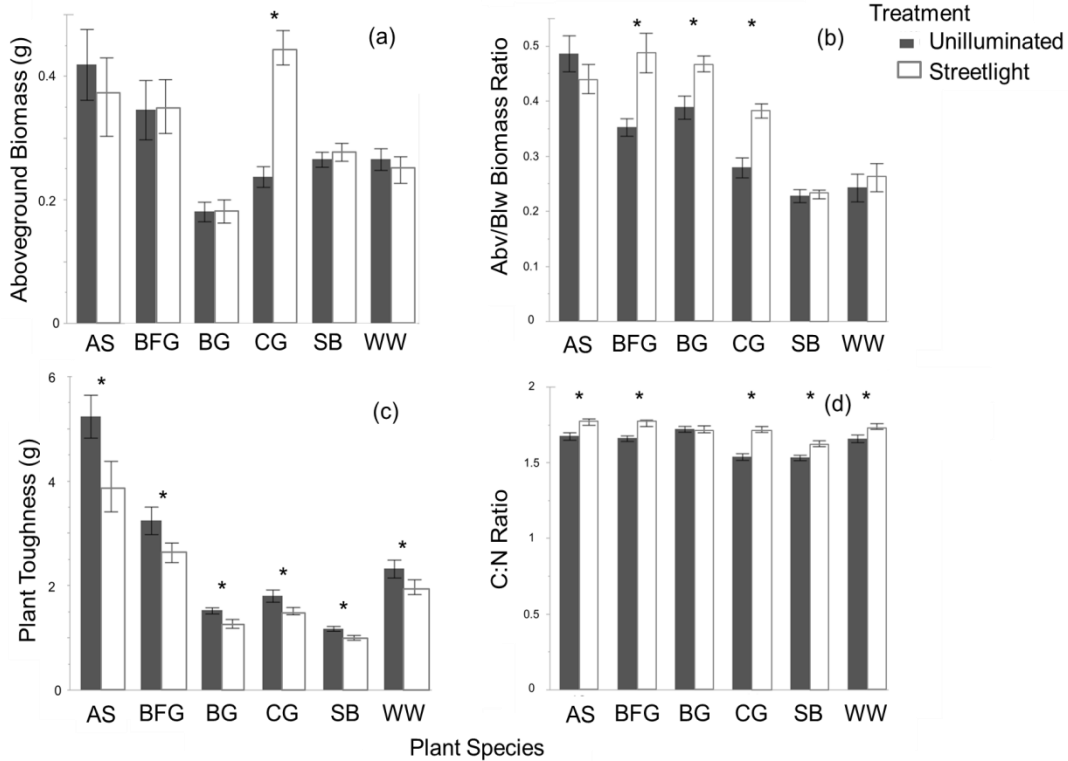
## Results

### Plant Performance - Greenhouse

Streetlights affected germination based on species (*treatment x species*:  $F_{5,348} = 3.27$ ,  $p = 0.007$ ; Appendix Figure B7). Streetlights did not affect germination rates of any of the species compared to the control treatment except buffalo grass, for which streetlights improved germination (Tukey's HSD test,  $p < 0.05$ ). We also found significant differences in germination rate among plant species (*species*:  $F_{5,348} = 160$ ,  $p < 0.0001$ ).

Streetlights improved aboveground biomass growth only for cheatgrass, an invasive species (*treatment x species*:  $F_{5,291} = 6.25$ ,  $p < 0.0001$ ; Figure 6a). However, when comparing the aboveground/belowground ratio, streetlights affected two native species, blue grama and buffalo grass, along with cheatgrass (*treatment x species*:  $F_{5,268} = 3.80$ ,  $p = 0.002$ ; Figure 6b); these three species invested more energy into aboveground biomass than belowground biomass when exposed to street lighting at night. Streetlight decreased plant toughness for all species (*treatment*:  $F_{1,272} = 20.72$ ,  $p < 0.0001$ ; Figure 6c) and toughness differed among plant species (*species*:  $F_{5,272} = 74.75$ ,  $p < 0.0001$ ; Figure

6c). Lastly, streetlights increased the C:N ratio for all species except blue grama ( $treatment \times species: F_{5,314} = 4.06, p = 0.0014$ ; Figure 6d); these five species had more carbon and less nitrogen per gram when exposed to streetlighting at night.



**Figure 6. Effects of streetlight exposure on (A) aboveground dry biomass by seedling, (B) aboveground/belowground biomass ratio, (C) plant toughness by seedling, and (D) C:N ratio of grass species grown in the greenhouse experiment. White bars indicate the streetlight treatment and gray bars are the control treatment. Bars show the mean of each measure  $\pm 1$  SE of root transformed data in A and C and log transformed data in B and D. Asterisks indicate significant differences between treatments ( $p < 0.05$ ). Native species: AS = alkali sacaton, BFG = buffalo grass, BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.**

To test whether streetlights affected these plant traits as plants aged, we tested the four species with multiple harvests for time effects. Only the invasive species cheatgrass grew larger in the streetlight treatment ( $treatment: F_{1,49} = 2.96, p < 0.0001$ ; Appendix

Figure B8) but did not change over time. Blue grama and smooth brome both increased aboveground biomass over time (blue grama *harvest*:  $F_{5,48} = 5.56$ ,  $p = 0.0004$ ; smooth brome *harvest*:  $F_{5,48} = 9.94$ ,  $p < 0.0001$ ; Appendix Figure B8) but showed no difference in growth between the light treatments (Appendix Figure B8). There was no difference in either harvest or treatment for aboveground biomass in western wheatgrass (Appendix Figure B).

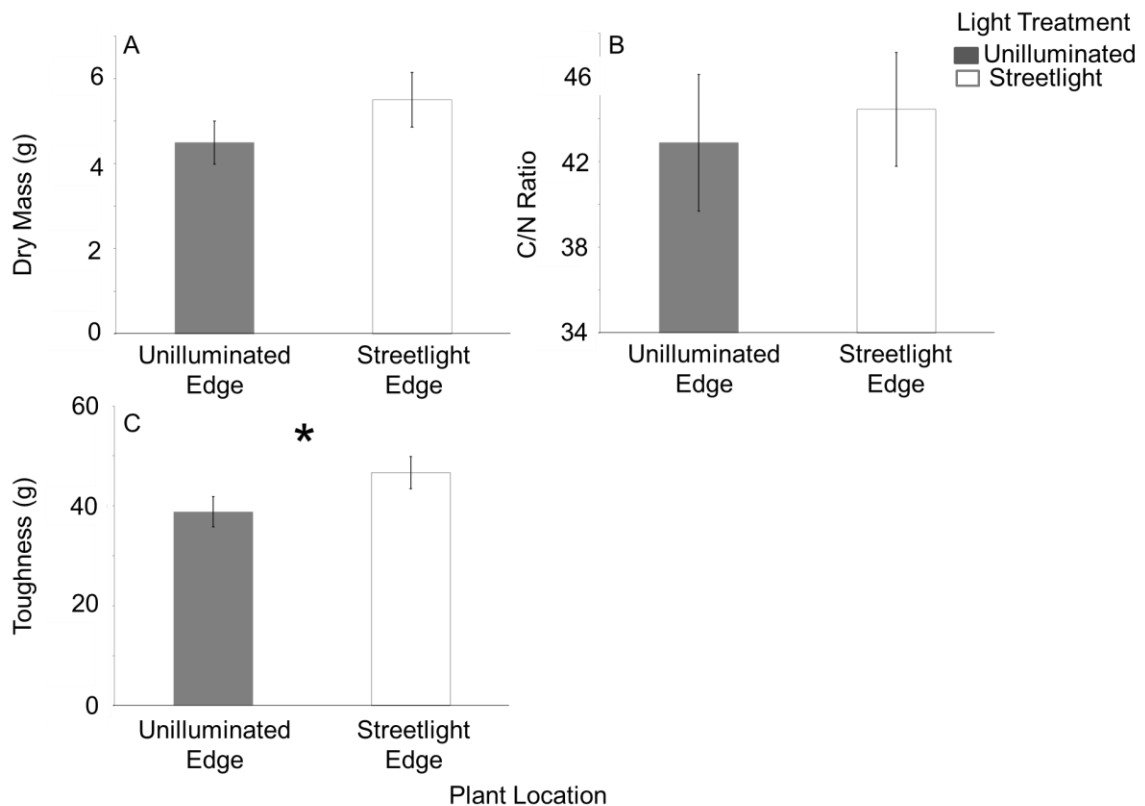
The native species blue grama and invasive species cheatgrass showed a larger above/belowground biomass ratio in the streetlight treatment (blue grama *treatment*:  $F_{1,49} = 6.56$ ,  $p = 0.015$ ; cheatgrass *treatment*:  $F_{1,53} = 18.36$ ,  $p < 0.0001$ ; Appendix Figure B9) but did not change over time. Only the invasive species smooth brome showed an increase over time in above/belowground biomass ratio (*harvest*:  $F_{5,48} = 6.44$ ,  $p = 0.0001$ ; Appendix Figure B9) but showed no difference in growth between the light treatments (Appendix Figure B9). There was no difference in either harvest or treatment for biomass in western wheatgrass (Appendix Figure B9).

Streetlights decreased leaf toughness and the effect of streetlights on toughness did not change over time for invasive smooth brome (*treatment*:  $F_{3,32} = 6.53$ ,  $p = 0.016$ ; Appendix Figure B10). Toughness differed over time for blue grama (*harvest*:  $F_{4,40} = 10.80$ ,  $p < 0.0001$ ) and decreased with streetlights (*treatment*:  $F_{1,40} = 8.53$ ,  $p = 0.006$ ) but the two variables did not interact. Toughness differed over time for western wheatgrass (*harvest*:  $F_{5,46} = 2.87$ ,  $p = 0.025$ ), and was nearly less tough in the streetlight treatment (*treatment*:  $F_{1,46} = 3.77$ ,  $p = 0.058$ ; Appendix Figure B10). Toughness did not change over time or by treatment in cheatgrass.

We also discovered that some plant species exposed to artificial lighting at night contained less nitrogen, and thus had a higher C:N ratio, than plants grown in the control treatment and that the C:N ratio changed over time (cheatgrass *treatment*:  $F_{1,48} = 46.80$ ,  $p < 0.0001$ , *harvest*:  $F_{5,48} = 3.59$ ,  $p = 0.008$ ; Appendix Figure B11). Others only responded to the light treatment (smooth brome *treatment*:  $F_{1,48} = 13.51$ ,  $p = 0.0006$ ; western wheatgrass *treatment*:  $F_{1,46} = 5.70$ ,  $p = 0.021$ ; Appendix Figure B11). However, there was an interaction between *treatment* and *harvest* for blue grama ( $F_{5,46} = 4.62$ ,  $p = 0.002$ ; Appendix Figure B11); plants grown under streetlights only had more carbon and less nitrogen later in development (after the third harvest).

#### Plant Performance – Field

For the smooth brome plants we collected from the field, there were no differences in aboveground biomass and C:N ratio for plants collected from under streetlights or the unilluminated edge (aboveground:  $F_{1,21} = 0.7$ ,  $p = 0.4$ ; C:N ratio:  $F_{1,20} = 0.9$ ,  $p = 0.3$ ; Figure 7a, b). However, plants in the field did differ in toughness; plants growing under streetlights were tougher than those growing along unilluminated edges ( $F_{1,21} = 4.89$ ,  $p = 0.04$ ; Figure 7c). Site was not significant in any of these analyses.



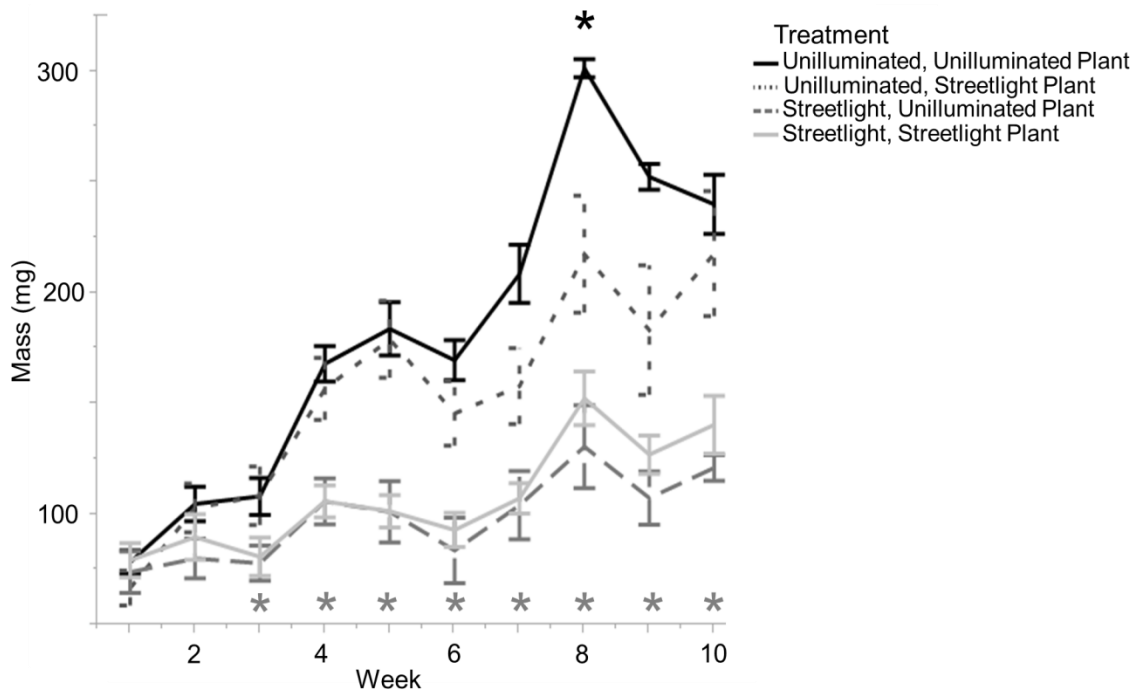
**Figure 7. Effects of streetlight exposure on (A) above-ground dry biomass, (B) C:N ratio, and (C) plant toughness of smooth brome collected in the field. White bars indicate plants collected under streetlights and gray bars represent plants collected from unilluminated edges. Bars show the mean of each measure  $\pm 1$  SE. Asterisks indicate significant differences between treatments ( $p < 0.05$ ).**

### Herbivore Performance

All larvae in the four treatments of our full factorial experiment started out at similar sizes based on body length ( $F_{3,144} = 0.96$ ,  $p = 0.4$ ). Larval survival did not differ among the four treatments for either host plant or light treatment (Log-Rank  $\chi^2 = 1.88$ ,  $df = 3$ ,  $p = 0.6$ ).

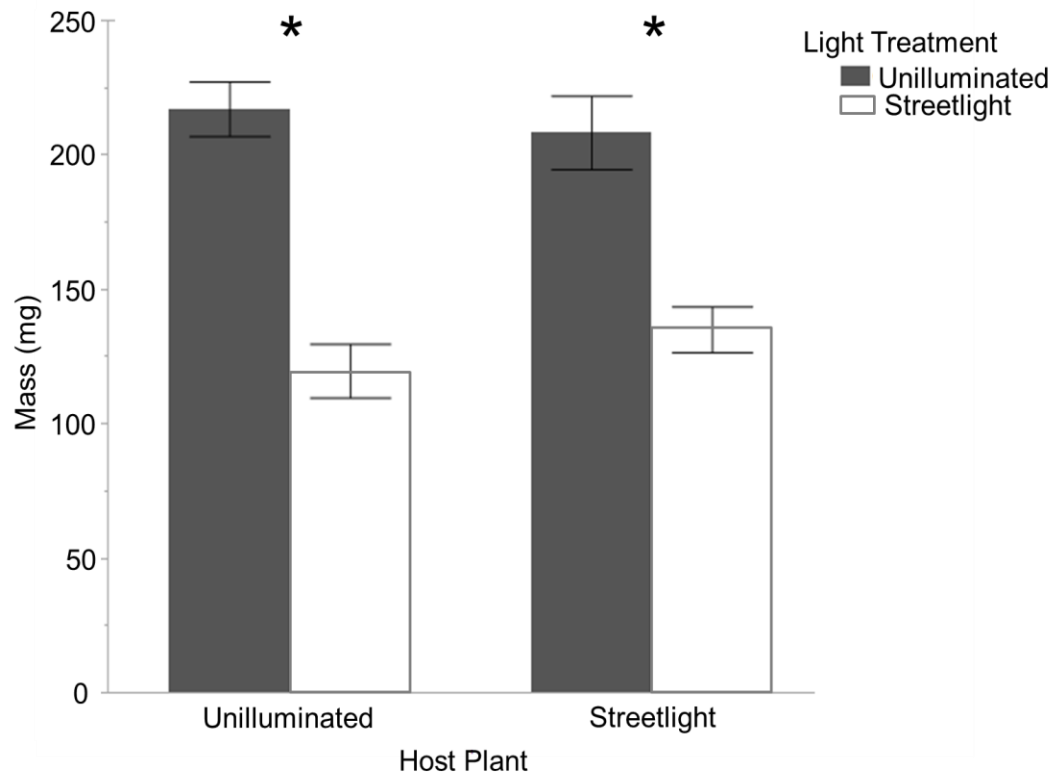
For larval body mass, we found a marginally significant three-way interaction between light treatment (streetlights vs. unilluminated in greenhouse), host plant

treatment (plants collected under streetlights vs. unilluminated in field) and time ( $F_{2,43,58,29} = 2.74$ ,  $p = 0.06$ ). After week 2, the larvae in the unilluminated conditions gained more mass than larvae in the streetlight treatment and continued to have greater body mass for the duration of the experiment (*time x treatment*:  $F_{2,43,58,29} = 15.37$ ,  $p < 0.0001$ ; Figure 8). At week 8 in the experiment, larvae feeding on unilluminated host plants had gained more mass than larvae feeding on streetlight host plants, but only in the unilluminated treatment (Figure 8).



**Figure 8. Effects of both streetlight exposure and host plant location on larval mass accumulation. The lines show the mean mass at each time point  $\pm$  1 SE in each of the four combinations of light treatment (unilluminated or streetlight) and host plant treatment (unilluminated or streetlight). The gray asterisks show time points that were significantly different between unilluminated and streetlight conditions and the black asterisk indicates the time point when larval mass differed significantly by host plant treatment (unilluminated and streetlight) in the unilluminated condition.**

However, the final mass of all larvae did not show any host plant effects; larvae growing under streetlights were smaller than their conspecifics growing under unilluminated conditions regardless of whether they were reared on host plants collected from streetlight or unilluminated habitats ( $F_{1,67} = 47.62$ ,  $p < 0.0001$ ; Figure 9).



**Figure 9. Mean larval mass ( $\pm 1$  SE) after 10 weeks reared in unilluminated or illuminated conditions and on host plants collected under unilluminated or illuminated conditions. The gray bars indicate larvae reared in unilluminated conditions and the white bars represent larvae reared in the streetlight treatment. Asterisks indicate significant differences between light environment treatments.**

## Discussion

Our study demonstrates that light pollution may be a disturbance that favors the growth of invasive plant species and also affects plant traits that are important to herbivores. Our greenhouse study showed a significant difference in how plant species respond to streetlights. The native species alkali sacaton and western wheatgrass altered few traits in response to streetlight conditions whereas two other native species (blue grama and buffalo grass) and both invasive species (cheatgrass and smooth brome) exhibited many differences between the streetlight and control treatments. We found that cheatgrass, which is listed as highly invasive in the US (Skinner et al. 2008), grew significantly larger under streetlights than in unilluminated conditions and grew larger than native plants either under streetlights or not. However, none of the native species nor the other invasive species that we tested (smooth brome) responded as positively to streetlights as cheatgrass, potentially due to differences in life history; cheatgrass is an annual plant whereas smooth brome is a perennial. Yet, if some invasive species, such as cheatgrass, grow larger under light polluted conditions, they may use resources more quickly to out-compete native species. Thus, streetlights may directly affect invasion dynamics in urban environments and light pollution may be an important disturbance that favors the growth of invasive plant species.

Plants grown under streetlight conditions in the greenhouse were significantly less tough and had higher C:N ratios than their conspecifics grown under ambient conditions. The precise mechanism by which streetlights affect plant physiology has not been tested



and remains unclear. Previous research has shown that plants exposed to longer photoperiods have different photosynthetic capabilities and changes in cellular processes important to photosynthesis (Briggs 2006; Raven, Evert, and Eichhorn 1986); alterations to photosynthetic pathways may reduce the amount of energy available for secondary metabolism (plant defense traits) or nutrient uptake. Regardless of the mechanism, changes to plant traits like toughness and C:N ratio are important as they affect host plant quality for invertebrate herbivores (Schoonhoven, van Loon, and Dicke 2005; Price et al. 2011). Plant toughness is a physical defense that can decrease the amount of plant material herbivorous insects are capable of consuming by wearing down insect mandibles (Schoonhoven, van Loon, and Dicke 2005; Massey and Hartley 2009). If an herbivorous insect spends more time tearing through plant material to feed, it will not consume the plant as quickly and is exposed to predators longer, thereby increasing plant fitness and decreasing herbivore fitness (Bernays 1997). Conversely, plants that are less tough are easier to feed upon, allowing insects to consume more plant material in shorter amounts of time. Our greenhouse results show that plants grown under streetlights may be easier to consume by herbivores because they are less tough, but the higher C:N ratio suggests that they need to consume more plant material to obtain the same amount of nitrogen as contained in plants not under streetlights. Although plants grown under streetlight conditions may be easier to consume, they may not be a better host plant due to the lower levels of nitrogen, suggesting that streetlights create a trade-off for invertebrate herbivores between consumption ability and nutrition. This trade-off may lessen the indirect effect of streetlights on herbivore fitness mediated through host plants.

We found that smooth brome plants grown in the field under streetlights responded differently to streetlights than the seedlings in our greenhouse study and this result may be due to plant age or environmental conditions in the field. Smooth brome grown under streetlights in the greenhouse were less tough than those grown in ambient conditions; yet, in the field, plants growing under streetlights were tougher than conspecifics growing along unilluminated edges and seven times tougher than those in the greenhouse. Given that plants in our greenhouse study were seedlings and plants in the field could be several years old, plants may also have different responses to streetlights as they age. Differences in how plants responded in the field vs. greenhouse could also be due to variation in soil conditions in the field between streetlight and unilluminated treatments that were unrelated to the lights themselves. For instance, when installing streetlights, the soil is compacted by the construction equipment whereas soils along the unilluminated edge may also have been compacted to some degree, but not as much. Additionally, because we found no difference in C:N ratio in the field between lit and unlit plants, there is no trade-off between plant toughness and C:N ratio in the field plants. Thus, individuals of this invasive plant species growing under streetlights in the field are more resistant to insect herbivores because they are both tougher and have lower nitrogen content, which would likely affect invasion dynamics. Future studies should test additional plant species in the field to determine whether other plant species respond similarly to streetlights as smooth brome and whether differences in herbivore consumption ability have fitness effects on the plants themselves.

Our larval performance study demonstrates that streetlights affect larval performance both directly and indirectly via induced changes in host plant quality. We found that larvae reared under streetlights weighed 43% less than larvae reared under unilluminated conditions; light pollution thus has a direct negative effect on larval fitness. Body mass is an accepted proxy for lifetime fitness in many Lepidoptera (Schoonhoven, van Loon, and Dicke 2005; Price et al. 2011). Because the direct effect of light pollution on larval mass was so strong, this could have serious impacts for larvae developing under streetlights. First, larvae with low body mass translate into adults with fewer resources for finding mates and producing offspring (Loewy et al. 2013). Second, larvae with less mass may need to spend more development time as larvae before pupating (Schoonhoven, van Loon, and Dicke 2005; Price et al. 2011); however, our study is limited because we did not measure growth rate between instars, only between weeks which limits the evidence for slow growth/high mortality hypothesis. The larval stage has the highest amount of mortality and exposes larvae to predators for a longer period of time (Varley and Gradwell 1960; Clancy and Price 1987). It is worth noting that although light pollution does not directly increase predation rate on larvae in our system (Grenis, Tjossem, and Murphy 2015), streetlights may indirectly increase mortality from predators by increasing larval development time and thus increasing their exposure time to predators. Therefore, light pollution can have detrimental fitness impacts on both larvae developing under streetlights and for those adults that lay eggs near streetlights.

We also found that streetlights can affect larval performance indirectly, via effects on host plant. Larvae reared under unilluminated conditions and fed host plants that we

collected from under streetlights had lower body mass than larvae consuming plants from unilluminated conditions. Our results show that streetlights indirectly decreased larval fitness via changes in host plant quality as plants collected from under streetlights in the field were tougher than those not under streetlights. Additionally, these plant changes appear to vary in importance during different points in larval development. Notably, we only found host-plant mediated differences in fitness in the unilluminated treatment, perhaps because the direct, negative effect of streetlights was so large, but larvae in the field would not encounter similar conditions as streetlight plants exist only under streetlights. Overall, our results show that streetlights can have both direct and indirect negative effects on herbivore fitness.

In summary, we found that light pollution alters plant traits important in at least two types of species interactions: competition and herbivory. Streetlights facilitate growth of an invasive species in our system, potentially affecting competitive interactions between native and exotic plants. Additionally, streetlights have both direct and indirect impacts on herbivores; larvae are smaller when reared under streetlights (direct), and streetlights change plant traits that lead to less larval growth (indirect). Our results provide evidence that the impacts of ecological light pollution in the environment have the potential to alter community dynamics through species interactions. While our study presents an important first step, these interactions should be investigated in the field as well to determine to what extent light pollution can alter natural communities and species interactions.

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## **APPENDIX A: AN ALTERNATE METHOD FOR COLLECTING NOCTURNAL INSECTS IN TREE-LESS HABITATS**

Black light collecting sheet set ups are considered a standard technique for collecting nocturnal insects and are used by researchers and amateur collectors alike. Many guides suggest using a 15 watt ultraviolet light with a sheet for insects to rest upon (Powell and Opler 2009; Covell 2005). In forested habitats, sheets can be easily be hung by tying a rope between two trees, draping the sheet over the rope, and securing it with clothespins. However, this technique for hanging a sheet is not feasible when collecting in habitats without tall, sturdy vegetation upon which to tie a sheet using the rope and clothespin method. Commercial pop-up sheets are available for collecting in flat areas, but they are expensive and can deplete limited funds unnecessarily. I have devised a new method for constructing a low-cost frame on which to hang a twin sheet; the frame can be constructed with materials from any local hardware store for less than \$30.

The frame consists of a total of 9.1 m of 1.9 cm ( $\frac{3}{4}$  inch) polyvinyl chloride (PVC) pipe (measurement also given in English units in parentheses as this is how PVC pipe is labeled for commercial sale in the United States). The PVC pipe needs to be cut into twelve pieces and trimmed to the measurements given in Appendix Table A1. I have determined that a chop saw is the easiest method for cutting the PVC pipe, but a hand saw or PVC pipe cutter will work as well. Additional materials that are necessary are: one straight PVC pipe connector, two 90-degree PVC pipe connectors, six 'T' shape PVC pipe connectors, and a fitted sheet for a twin bed. Tent stakes may also be purchased to anchor the frame to the ground if collection takes place in a windy environment.

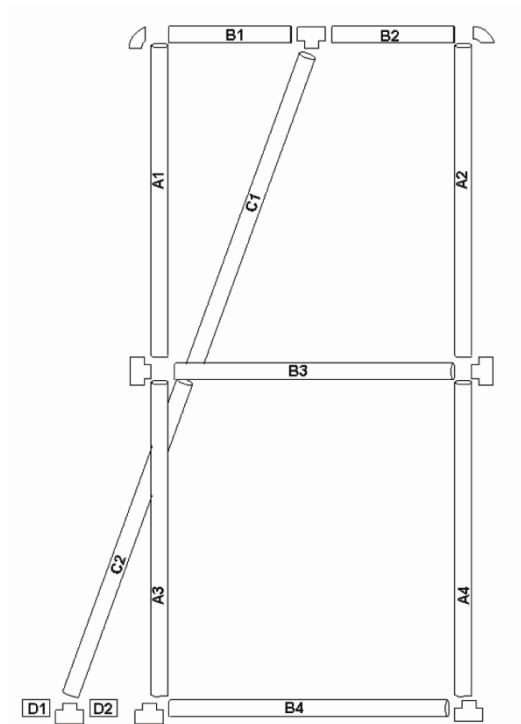
To assemble the frame, connect the A and B PVC pipe pieces to form the façade of the frame (Appendix Figure A1). The C and D PVC pipe pieces form the rear support for the façade and attach to the top of the frame at a  $\sim 25^\circ$  angle to the plane of the façade (Appendix Figure A2). After assembling the frame, a fitted twin sheet can be slipped over the frame and the tent stakes can be used to anchor pieces B4, D1, and D2 to the ground. The black light battery can also be used to weigh the frame down by resting it on piece B4. When ready to begin collecting, simply drape the black light over the top of the frame (Appendix Figure A3).

There are several advantages to this frame over the commercial versions that are available. First, it is made entirely of pieces that can be found in any local hardware store. Second, the entire cost of the frame is less than \$30 and thus is an affordable option for collectors of more limited means (e.g. graduate students and amateur collectors). Finally, the frame, as I have designed it, is light and weighs about four pounds. Thus, when disassembled, the entire frame can be carried in a large mesh laundry sack and is easy to transport over rough terrain and long distances.

**Appendix Table A1. Lengths of PVC pipe necessary to make a frame that will be sized to fit a fitted twin sheet.**

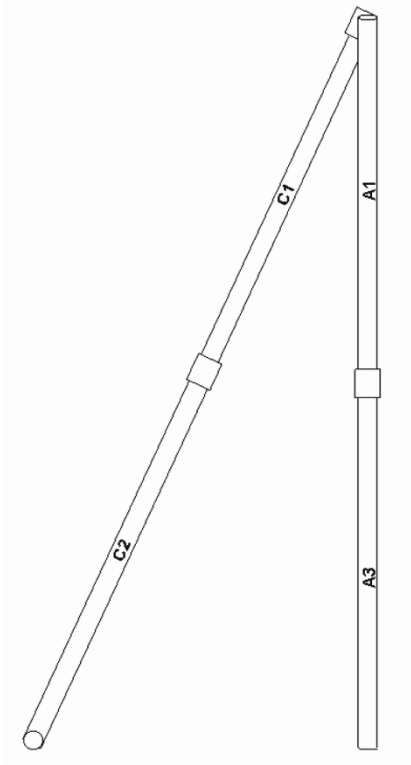
| <b>Poles</b>   | <b>Length (cm)</b> |
|----------------|--------------------|
| A1, A2, A3, A4 | 89                 |
| B1, B2         | 49                 |
| B3, B4         | 104                |
| C1, C2         | 111                |
| D1, D2         | 13                 |

**Appendix Figure A1. Frame Assembly from front view.**





**Appendix Figure A2. Frame Assembly from side view.**



## APPENDIX B: SUPPLEMENTARY TABLES AND FIGURES

**Appendix Table B1. Site name and abbreviation for Figure 2, county, collection dates, species caught, individual-based estimation of species richness, and estimate of total moth diversity for all sites used in our 2011-2012 moth collections.**

| Site           | County     | Lat         | Long         | Month-Year Sampled | Species Richness | Abundance-Corrected Species Richness | Estimated Species Richness |
|----------------|------------|-------------|--------------|--------------------|------------------|--------------------------------------|----------------------------|
| Aquarius       | Boulder    | 39.974358   | -105.112252  | July 2011          | 36               | 9.25                                 | 76                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Coyote Run     | Boulder    | 39.98225    | -105.14976   | August 2012        | 43               | 9.88                                 | 73                         |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
| Warembourg     | Boulder    | 39.97067412 | -105.1449108 | July 2012          | 36               | 7.98                                 | 65                         |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
| Red Fox        | Boulder    | 40.059187   | -105.193019  | June 2012          | 28               | 8.75                                 | 78                         |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Twin Lakes     | Boulder    | 40.059721   | -105.201784  | August 2012        | 30               | 9.77                                 | 144                        |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Forest Park    | Arapahoe   | 39.574799   | -104.94956   | July 2011          | 18               | 6.57                                 | 27                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Holly Park     | Arapahoe   | 39.596893   | -104.920764  | August 2012        | 27               | 9.77                                 | 49                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Horseshoe Park | Arapahoe   | 39.579894   | -104.995126  | August 2012        | 25               | 9.68                                 | 36                         |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Jackass Hill   | Arapahoe   | 39.581845   | -105.018353  | June 2012          | 12               | 7.95                                 | 32                         |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Willow Springs | Arapahoe   | 39.587038   | -104.917331  | June 2012          | 22               | 7.08                                 | 61                         |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Crown Hill     | Jefferson  | 39.761047   | -105.101995  | July 2011          | 31               | 10.15                                | 86                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
| Loveland Trail | Jefferson  | 39.675633   | -105.150661  | July 2011          | 56               | 10.65                                | 84                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Ravines        | Jefferson  | 39.683643   | -105.139847  | August 2012        | 76               | 10.74                                | 135                        |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
| Ute Trail      | Jefferson  | 39.679811   | -105.150962  | July 2012          | 66               | 10.64                                | 127                        |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
| Welchester     | Jefferson  | 39.730426   | -105.143538  | June 2012          | 36               | 8.8                                  | 138                        |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| CC             | Adams      | 39.904989   | -105.037786  | August 2012        | 12               | 9.26                                 | 34                         |
|                |            |             |              | July 2012          |                  |                                      |                            |
| East Lake      | Adams      | 39.919315   | -104.95647   | June 2012          | 30               | 9.96                                 | 43                         |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Glen Eagle     | Adams      | 39.929978   | -104.886904  | July 2011          | 37               | 10.22                                | 77                         |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Mountain View  | Adams      | 39.886153   | -105.029074  | June 2012          | 10               | 10.74                                | 27                         |
|                |            |             |              | August 2012        |                  |                                      |                            |
| Mushroom Ponds | Adams      | 39.893851   | -105.02198   | July 2011          | 23               | 8.95                                 | 80                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
| Oscar Arnold   | Adams      | 39.89745654 | -105.0089121 | July 2011          | 38               | 9.73                                 | 74                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
| The Field      | Broomfield | 39.92593    | -105.065904  | July 2011          | 22               | 8.47                                 | 34                         |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
| Westcliff      | Adams      | 39.872808   | -105.065196  | August 2012        | 35               | 7.25                                 | 69                         |
|                |            |             |              | July 2011          |                  |                                      |                            |
|                |            |             |              | August 2011        |                  |                                      |                            |
|                |            |             |              | June 2012          |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |
|                |            |             |              | July 2012          |                  |                                      |                            |
|                |            |             |              | August 2012        |                  |                                      |                            |

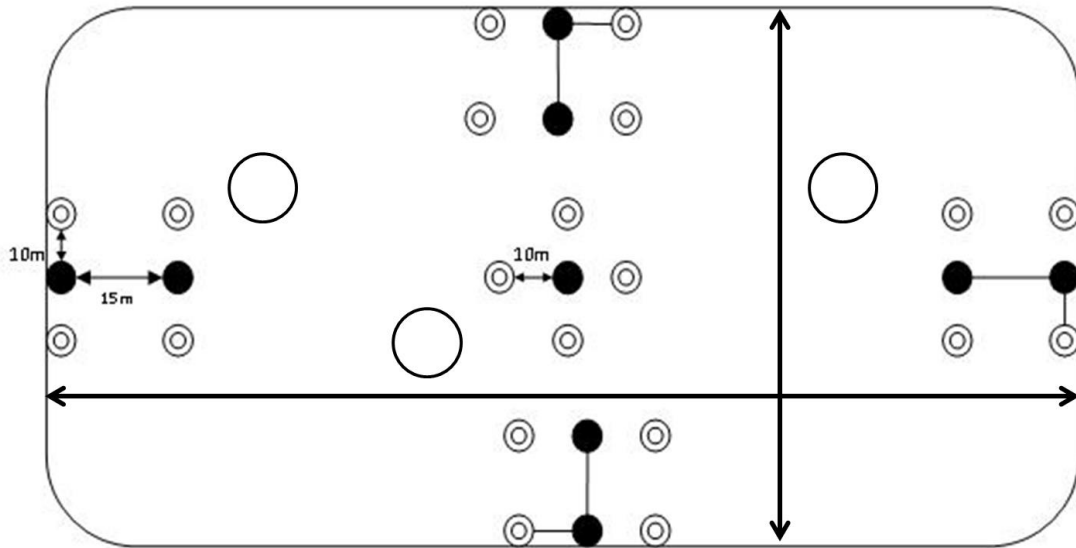
**Appendix Table B2. Abbreviations used for species in Figure 2, family, and species name of the 15 species with the highest species scores.**

| <b>Abbreviation</b> | <b>Family</b> | <b>Species</b>                      |
|---------------------|---------------|-------------------------------------|
| A_pha               | Erebidae      | <i>Apantesis phalerata</i>          |
| C_ere               | Erebidae      | <i>Caenurgina erechtea</i>          |
| D_pal               | Erebidae      | <i>Drasteria pallescens</i>         |
| G_bla               | Erebidae      | <i>Grammia blakei</i>               |
| V_fra               | Erebidae      | <i>Virbia fragilis</i>              |
| D_cur               | Geometridae   | <i>Digrammia curvata</i>            |
| D_nub               | Geometridae   | <i>Digrammia nublicata</i>          |
| A_tri               | Noctuidae     | <i>Anarta trifolii</i>              |
| A_dev               | Noctuidae     | <i>Apamea devastator</i>            |
| C_dis               | Noctuidae     | <i>Condica discistriga</i>          |
| E_alb               | Noctuidae     | <i>Euxoa albipennis</i>             |
| E_aux               | Noctuidae     | <i>Euxoa auxiliaris</i>             |
| E_obe               | Noctuidae     | <i>Euxoa obeliscoides</i>           |
| F_hel               | Noctuidae     | <i>Feltia herilis</i>               |
| F_jac               | Noctuidae     | <i>Feltia jaculifera</i>            |
| L_med               | Noctuidae     | <i>Lacinipolia meditata</i>         |
| L_str               | Noctuidae     | <i>Lacinipolia nr. strigicollis</i> |
| L_com               | Noctuidae     | <i>Leucania commoides</i>           |
| L_far               | Noctuidae     | <i>Leucania farcta</i>              |
| N_pro               | Noctuidae     | <i>Noctua pronuba</i>               |
| P_sau               | Noctuidae     | <i>Peridroma saucia</i>             |
| S_alb               | Noctuidae     | <i>Schinia albafascia</i>           |
| S_orn               | Noctuidae     | <i>Spodoptera ornithogalli</i>      |
| M_qui               | Sphingidae    | <i>Manduca quinquemaculata</i>      |

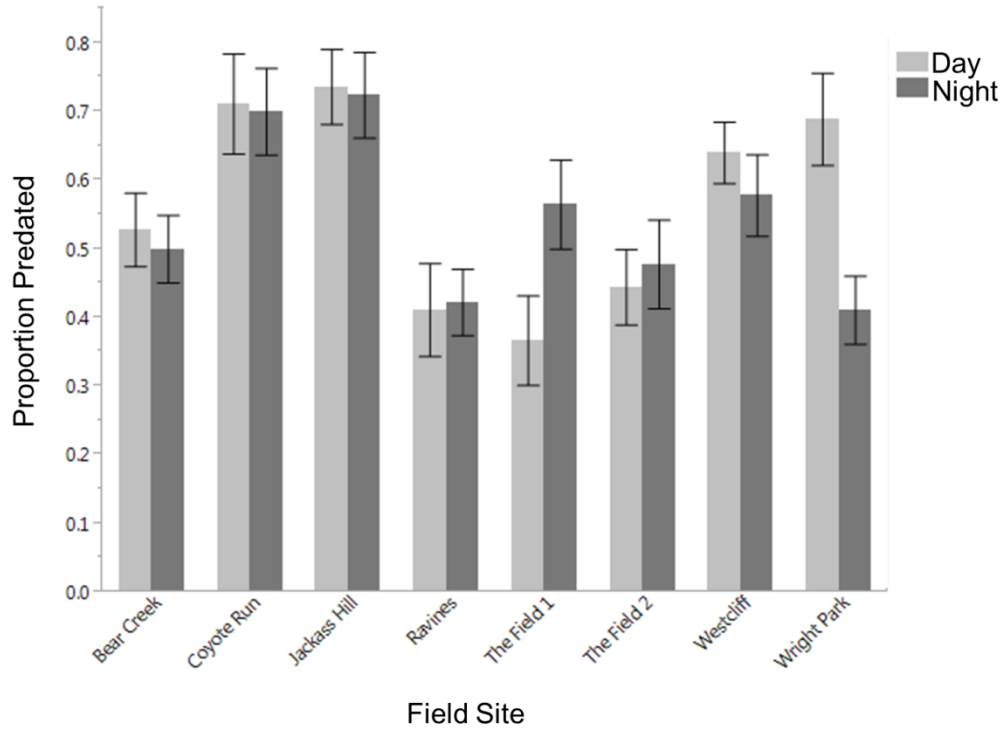
**Appendix Table B3: Field site name, area, location, and number of streetlights along the edge of the site.**

| <b>Site</b>  | <b>Area (ha)</b> | <b>Lat</b> | <b>Long</b> | <b>Streetlights</b> |
|--------------|------------------|------------|-------------|---------------------|
| Bear Creek   | 7.6              | 39.67823   | -105.1577   | 5                   |
| Coyote Run   | 10.3             | 39.98225   | -105.1497   | 3                   |
| The Field 1  | 7.2              | 39.92593   | -105.0659   | 5                   |
| The Field 2  | 14.9             | 39.92579   | -105.0655   | 5                   |
| Jackass Hill | 5.2              | 39.58185   | -105.0183   | 4                   |
| Ravines      | 14.5             | 39.68364   | -105.1398   | 5                   |
| Westcliff    | 6.5              | 39.87281   | -105.0652   | 3                   |
| Wright Park  | 6.1              | 39.68045   | -105.1355   | 2                   |

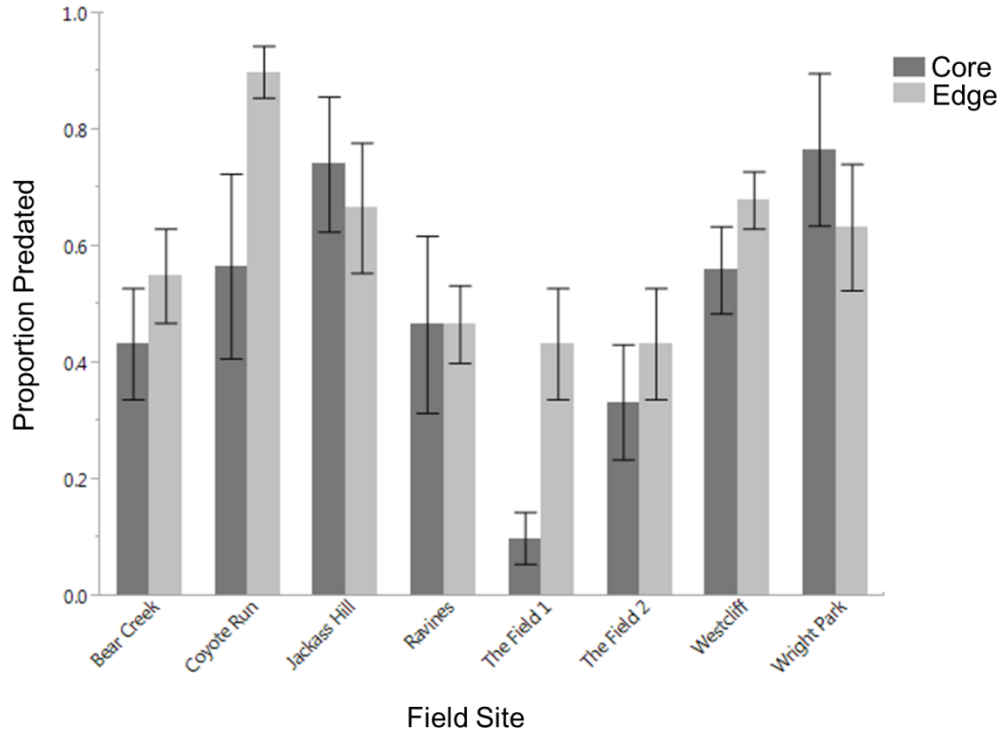
**Appendix Figure B1. Layout of ground cover survey and point measurements of light intensity.** The long dark arrows are the N-S and E-W transects. Open circles represent the transect around each trap location. We used a point-intercept line method to quantify ground cover at each site. Dark circles indicate the focal spot for light readings along the N, E, S, W, and center locations. Double circles show the position of additional light readings (10m from focal location along the edge and 15m into the patch).



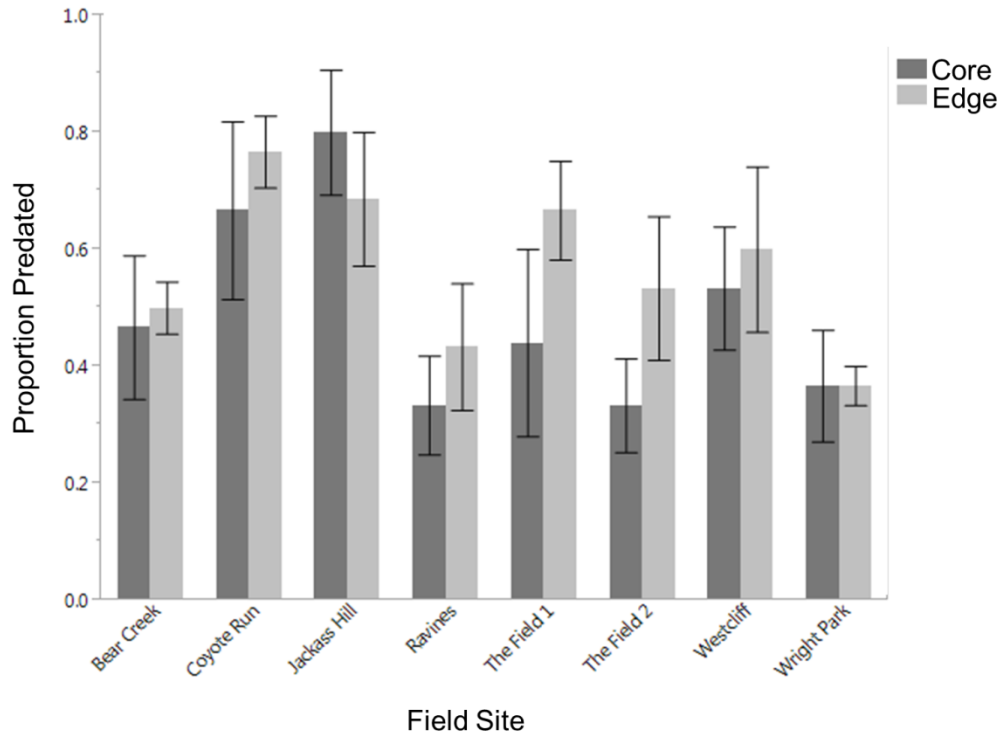
**Appendix Figure B2: Mean proportion of predated larvae ( $\pm 1$  SE) by field site during the day and night.**



**Appendix Figure B3: Mean proportion of predated larvae ( $\pm 1$  SE) by field site in the core and edge habitat during the day.**

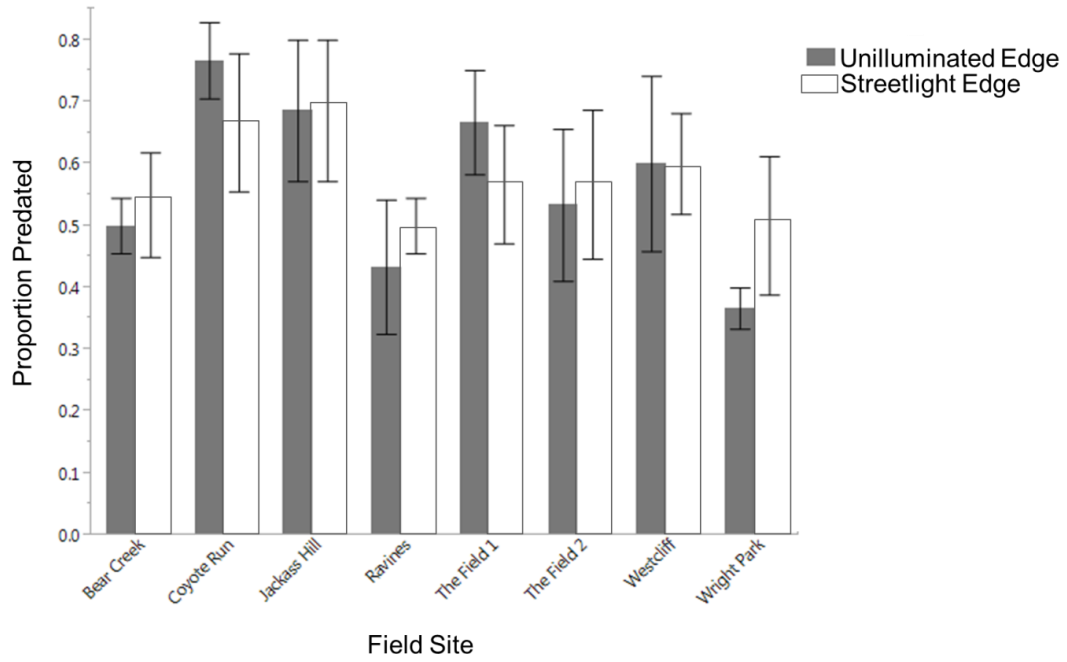


**Appendix Figure B4: Mean proportion of predated larvae ( $\pm 1$  SE) by field site in the core and edge habitat during the night.**

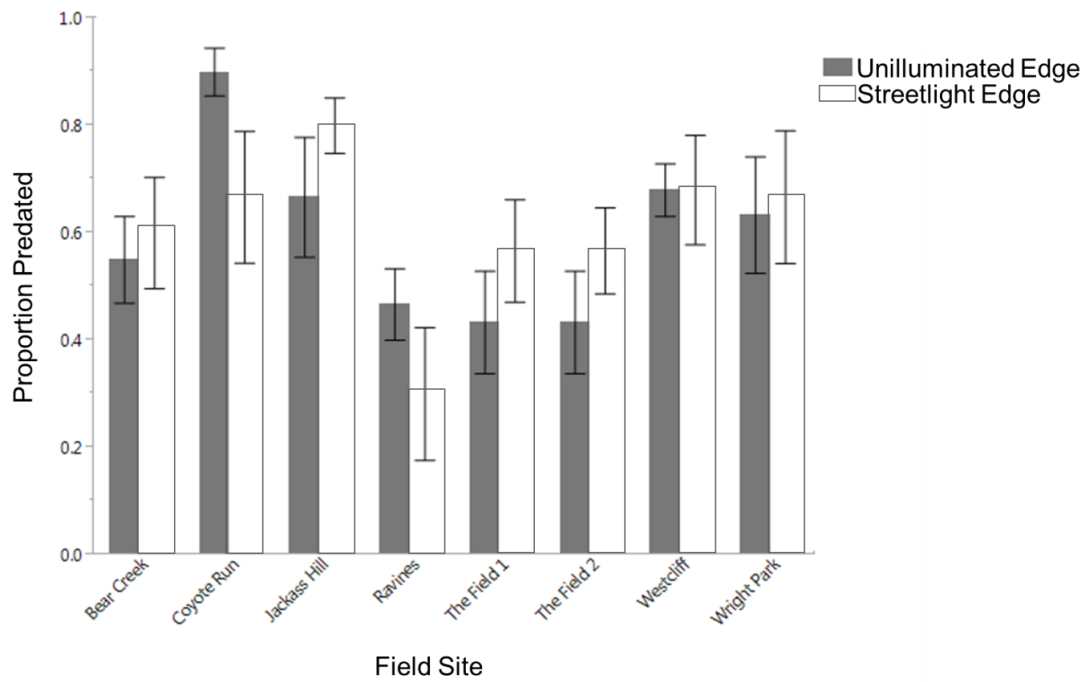




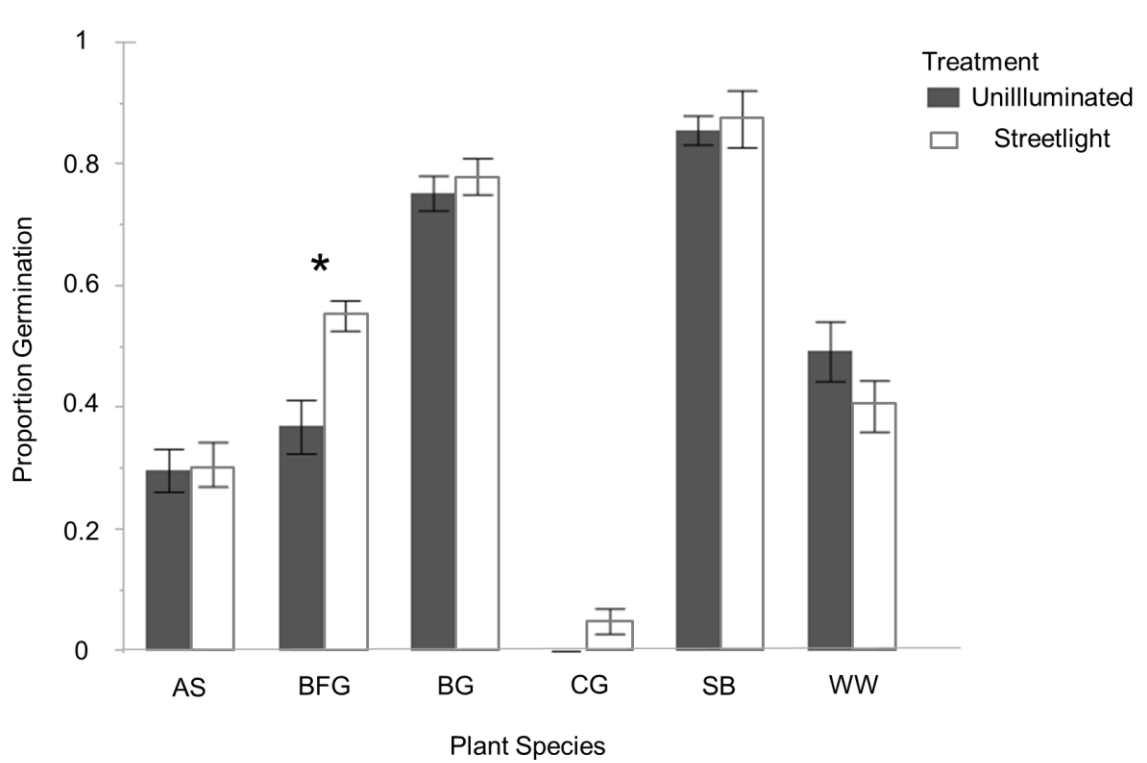
**Appendix Figure B5: Mean proportion of predated larvae ( $\pm 1$  SE) by field site in the unilluminated edge and streetlight edge habitat during the day.**



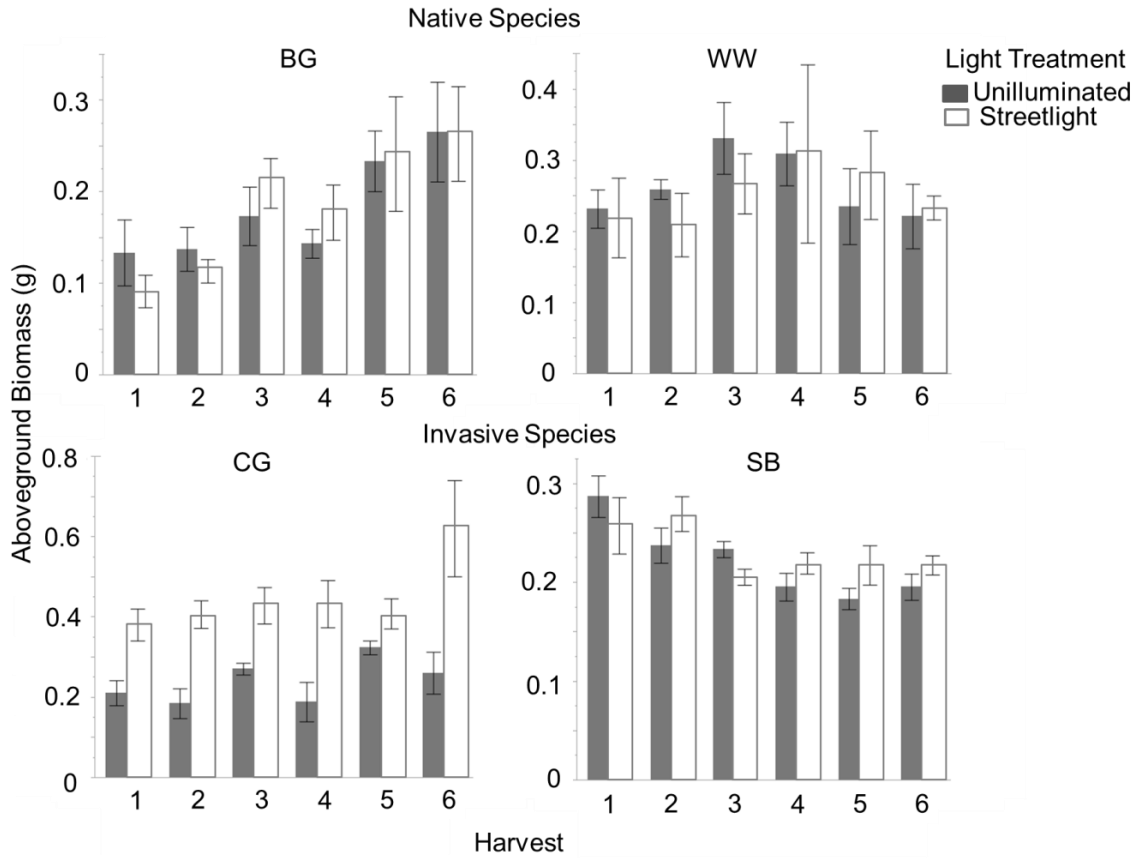
**Appendix Figure B6: Mean proportion of predated larvae ( $\pm 1$  SE) by field site in the unilluminated edge and streetlight edge habitat during the night.**



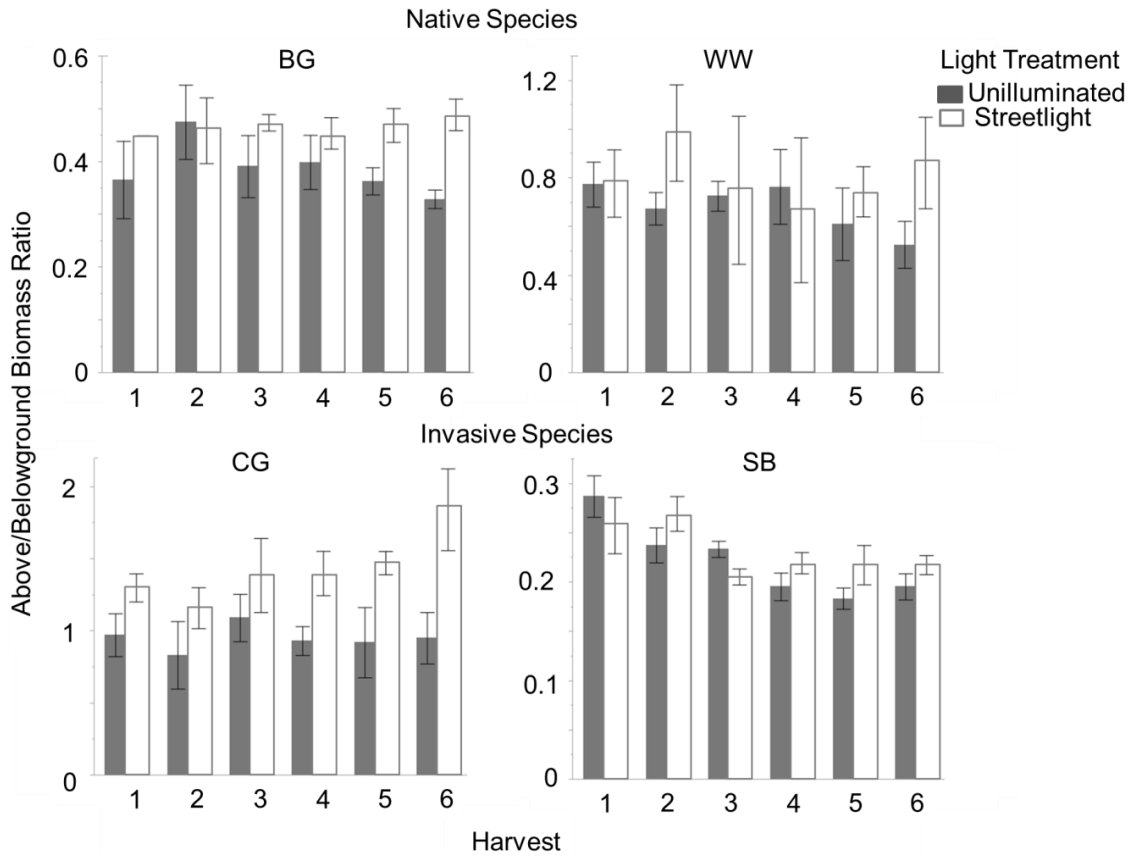
**Appendix Figure B7.** Mean ( $\pm 1$  SE) germination rate per cone-tainer in the unilluminated (gray bars) and streetlight (white bars) treatments after one month. Native species: AS = alkali sacaton, BG = blue grama, BFG = buffalograss, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.



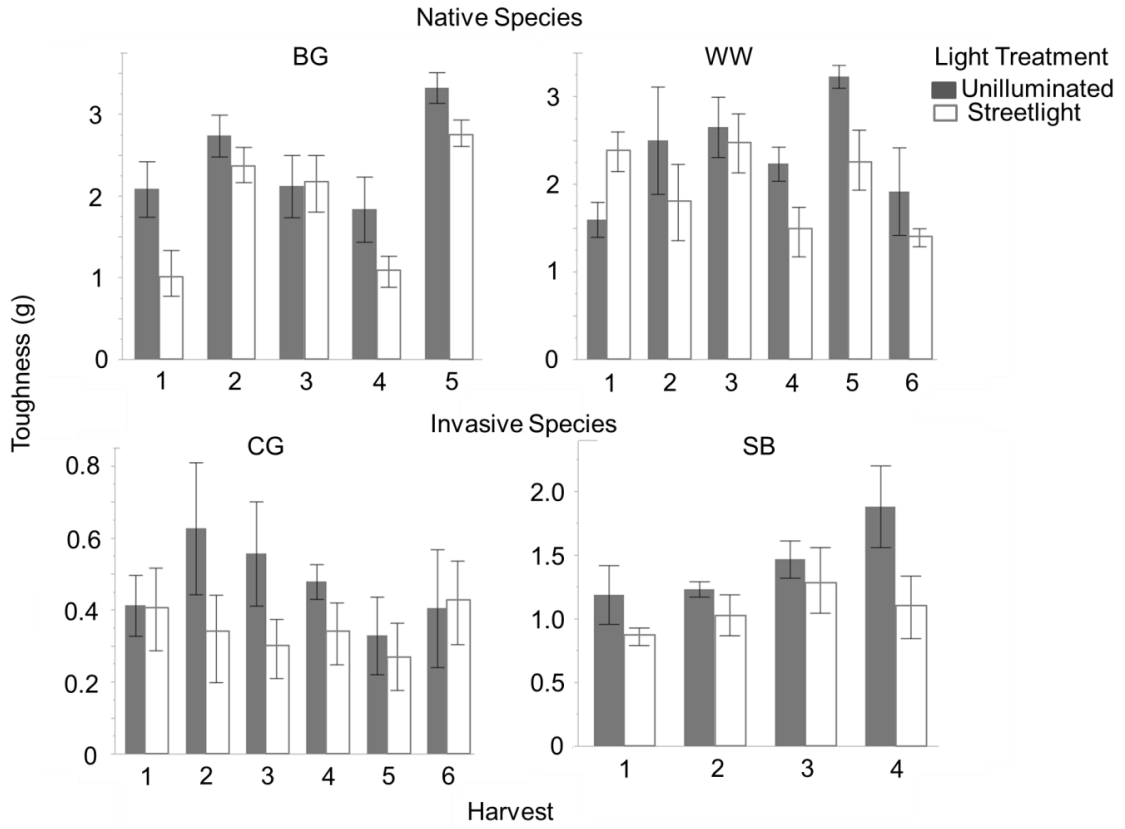
**Appendix Figure B8. Mean ( $\pm 1$  SE) aboveground biomass in the unilluminated (gray bars) and streetlight (white bars) treatments over the course of six harvests spanning 18 weeks. Native species: BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.**



**Appendix Figure B9. Mean ( $\pm 1$  SE) aboveground/belowground biomass ratio in the unilluminated (gray bars) and streetlight (white bars) treatments over the course of six harvests spanning 18 weeks. Native species: BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.**



**Appendix Figure B10. Mean ( $\pm 1$  SE) leaf toughness per cone-tainer in the unilluminated (gray bars) and streetlight (white bars) treatments over the course of six harvests spanning 18 weeks. We started toughness measures on Harvest 3 for smooth brome and Harvest 2 for blue grama when there was sufficient biomass. Native species: BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.**



**Appendix Figure B11. Mean ( $\pm 1$  SE) C:N ratio per cone-tainer in the unilluminated (gray bars) and streetlight (white bars) treatments over the course of six harvests spanning 18 weeks. Native species: BG = blue grama, WW = western wheatgrass. Invasive species: CG = cheatgrass, SB = smooth brome.**

