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**Title:** Direct and ambient light pollution alters recruitment for a diurnal plant-pollinator system

**Running title:** effects of light on yucca and moths

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## Abstract

Artificial light at night (ALAN) functions as a novel environmental stimulus that has the potential to disrupt interactions among species. Despite recent efforts to explain nocturnal pollinators' responses to this stimulus, the likelihood and associated mechanisms of attraction towards artificial light and potential consequences on fitness for diurnal pollinators is still largely unclear. Here, we took advantage of the obligate mutualism between yucca moths (*Tegeticula maculata maculata*) and yucca plants (*Hesperoyucca whipplei*) to understand how direct light exposure and skyglow can influence a pairwise plant-pollinator interaction. To surmise whether adult moths exhibit positive phototaxis, we deployed a set of field-placed light towers during the peak of yucca flowering and compared the number of moths caught in traps between dark-controlled and light-treated trials. Adult moth abundance was much higher

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when light was present, which suggests that ALAN may alter this diurnal moth's activity patterns to expand their temporal niche into the night. To evaluate ALAN effects on yucca fruit set and moth larva recruitment, we measured skyglow exposure above yucca plants and direct light intensity from a second set of light towers. Both larva and fruit recruitment increased with skyglow, and fruit set also increased with direct lighting, but the relationship was weaker. Contrarily, larva recruitment did not change when exposed to a gradient of direct light, which may instead reflect effects of ALAN on moth physiology, such as disrupted female oviposition, or misdirecting behaviors essential to oviposition activity. Our results suggest that ALAN can positively influence the fitness of both plants and moths in this tightly co-evolved mutualism, but the benefits to each species may depend on whether night lighting is direct or indirect. Whether such effects and mechanisms could relate to susceptibility to the presence of ALAN on this or other plant-pollinator relationships will remain an important focus of future research.

**Keywords:** Artificial light at night; positive phototaxis; diurnal pollinator; plant-pollinator communities; recruitment

## Introduction

Co-evolution between flowering plants and pollinators have shaped angiosperms to become the most speciose group of land plants on the planet (Ollerton 1996). Flowering plants have developed specialized features to balance the need to attract pollinators selecting for floral traits and mating systems, as well as constructing defense mechanisms to prevent herbivores, including pollinator larvae, from decimating plant reproductive output (Ramos and Schiestl 2019). Simultaneously, pollinators underwent behavioral and structural adaptations, such as altering the quantity and quality of flower visitation, features that increased efficiency of gathering and transferring pollen, or traits that increased the success of capitalizing on nutritious and / or reproductive benefits (Mitchell et al. 2009a). As such, the reciprocal advances in both plants and pollinators were a major promoter of evolutionary radiation and biodiversity (Ehrlich and Raven 1964). While pollination systems have persisted for millions of years, there is growing recognition that plant-pollinator interactions can be drastically influenced by anthropogenic changes to ecosystems, such as climate change, habitat fragmentation, and species' invasions (Mitchell et al. 2009b). The alteration of pollinator communities is likely to have cascading effects on plant population persistence, as pollinator decline intensifies pollen limitation, reduces plant reproductive success, and threatens the loss of genetic diversity (Thomann et al. 2013). One aspect of anthropogenic disturbances on plant-pollinator communities that has received little attention by researchers is the impact of artificial light at night (ALAN; Knop et al. 2017).

Within the last few decades, advances in lighting technology have caused the cost per unit brightness to fall and the intensity and quantity of light installations to increase exponentially, resulting in 2% annual growth in total light radiance globally (Kyba et al. 2017). This rate of growth exceeds the human population growth rate of 1.05% and is often ascribed to two primary factors: more light emitted per capita and a greater percentage of uplight from light fixtures (National Park Service 2017). Moreover, modern ALAN is no longer confined to urban centers; it radiates outwards along road networks that run through or around otherwise pristine areas (Buxton et al. 2020), and propagates as skyglow, which occurs

from atmospheric scattering of light (Kyba et al. 2015). Consequently, many natural systems experience considerable light pollution.

Natural light regimes are a fundamental organizing force in biology and regulate the timing of foraging, migration, circadian rhythms, and reproduction (Gaston et al. 2013, Seymoure et al. 2019a). However, ALAN dysregulates the amount, spectral conditions, and timing of light exposure (Gaston et al. 2017, Seymoure et al. 2019a). The consequence is that ALAN creates evolutionarily novel lighting conditions that differ strongly from those in which organisms have evolved (Seymoure et al. 2019b). As a result, some species may respond by changing their temporal use of habitat, which not only increases competition between crepuscular and nocturnal species, but also interferes with circadian cycles, among other effects (Gaston et al. 2013; Grubisic et al. 2019). Among plant pollinators, species that rely on visual cues may become disoriented, decrease vigilance for predators, decrease flowering-visiting activity, or suppress oviposition, resulting in an overall decrease in recruitment (Gaston et al. 2013, Macgregor et al. 2015, Owens et al. 2020). Furthermore, many nocturnal pollinators are naturally attracted to light sources and may experience increased predation from species that forage under longer periods of nocturnal illumination (Macgregor et al. 2015, Owens and Lewis 2018). Altered nocturnal pollinator behavior or declines in pollinator abundance could have consequences for the plants they pollinate (Macgregor et al. 2015). For example, an experimental study in Switzerland showed rural fields exposed to streetlights experienced a 29% decrease in nocturnal pollinator species composition, resulting in fewer pollinator visits by 62%, and subsequently a 13% reduction in fruit set (Knop et al. 2017). Furthermore, this reduction in the developmental process from flowers to mature plant reproductive output could indirectly affect diurnal pollinators by depleting a potential food source, decreasing network connectivity, and subsequently lowering plant diversity and altering the plant community composition (Fontaine et al. 2005). Yet, how responses to ALAN among diurnal pollinators directly influence the plants with which they interact is unknown.

Moths may be especially vulnerable to ALAN, as this stimulus can guide moths towards an incorrect target, often leading to a maladaptive response, or even increased mortality, in a process known

as misleading (Dominoni et al. 2020). Examples of misleading include interpreting artificial light sources as the moon (Baker and Sadovy 1978) or perceiving dark bands around sources of light as places of refuge, leading to non-stop flight patterns circling the light (Hsiao 1973). However, despite a recent meta-analysis regarding diurnal Lepidoptera species' attraction to sources of ALAN (van Langevelde et al. 2018), the mechanisms of attraction towards artificial light and potential consequences on fitness for diurnal pollinators is still largely unclear. To understand how the presence of ALAN influences the relationship between diurnal moths and their plant hosts, we investigated the effects of an artificial direct light treatment (henceforth “direct light”) and artificial indirect light from ambient skyglow (henceforth “skyglow”) on an obligate mutualism.

Flowers from yucca plants (*Yucca* and *Hesperoyucca* spp.) are only pollinated by their unique mutualist moths (*Tegeticula* and *Parategeticula* spp.), and likewise moths will only oviposit in yucca flower ovaries, which become a secure food source for the larvae (Baker 1986). As such, outside influences, such as other pollinator species or competing inflorescence plants, are eliminated in this closed plant-pollinator system. However, given the tight one-to-one relationship, the interaction is especially susceptible to destabilizing forces (Buchmann and Nabhan 2012), such as ALAN and other human-induced environmental conditions. Furthermore, while yucca moths within the *Tegeticula yuccasella* complex evolved to become active at night, *T. maculata* is one of three species that remained a diurnal pollinator (Powell and Mackie 1966; Pellmyr et al. 2008). Therefore, by introducing two external variables to the closed interaction between *T. maculata* and its mutualist yucca plant, we were able to directly measure the influence of direct light and skyglow on the behavioral response of a diurnal pollinator and the consequences for the host.

Using field-placed light manipulations at sites exposed to a gradient of skyglow, we investigated the influence of direct and indirect light on the yucca-yucca moth mutualism by quantifying chaparral yucca (*Hesperoyucca whipplei*) fruit set and the obligate moth (*Tegeticula maculata maculata*) larval density per fruit. Exposure to ALAN is known to influence a variety of behaviors among insects (Macgregor et al. 2015, Owens and Lewis 2018) and could result in disrupted melatonin synthesis, and

subsequently a cascade of adverse effects such as decreased sex pheromone production, sterility, and ultimately inhibiting reproductive output (Desouhant et al. 2019). Therefore, we predicted that the presence of direct artificial light would disrupt pollination and oviposition activity (Macgregor et al. 2015), resulting in a decrease in mature fruit per plant and fewer moth larvae per fruit. Conversely, because skyglow is diffusely spread in the night sky and contributes minimally to scene luminance when compared to direct light sources, skyglow is likely to influence moth reproductive output through other mechanisms. The presence of skyglow in a naturally dark environment may mislead diurnal moths by altering their perception of photoperiod, positively masking the nocturnal environment, and thereby increasing nocturnal activity and opportunities to reproduce (Macgregor et al. 2015, Desouhant et al. 2019). Therefore, we predicted yucca fruit set and moth larvae per fruit will increase with the intensity of indirect light from skyglow. Finally, by exploring potential evolutionary and physiological mechanisms to the measured responses, we can enhance our understanding of the consequences of direct and ambient artificial light for diurnal plant-pollinator systems (Dominoni et al. 2020).

## Methods

### *Study species*

We studied chaparral yucca plants (*Hesperoyucca whipplei*) and yucca moths (*Tegeticula maculata maculata*) in natural areas surrounding San Luis Obispo, California. Individual plants grow as rosettes for several years and then bloom in the spring, sending up a single, large, paniculate inflorescence that reaches 1.4-4 meters in height. Each flower remains open for several days, and an individual plant may continue to open flowers for as long as ten weeks (Aker and Udovic 1981). Yucca moths tend to be abundant wherever their obligate host plant is found. As moth adults only live for a few days and do not feed as adults, they have evolved unique tentacles on their maxillary palps to actively collect and compact pollen from the flowers of their yucca hosts (Aker and Udovic 1981). This direct fertilization ensures the flower will mature into a fruit pod and produce seeds, ensuring the future recruitment of the plant, while

providing a viable food source for moth larvae. Once the eggs are secured inside the flower's ovary, the larvae hatch inside the developing fruit and consume seeds within their immediate vicinity. As the pods begin to harden and are ready to dehisce, full-grown larvae bore out of the pods and descend to the ground, form cocoons under the soil, and wait for an environmental cue to pupate and emerge as adults (Baker 1986).

### *Experimental design*

We selected five sites with abundant yucca at the start of the flowering season in April 2019 (Supplementary material Appendix 1 Fig. A1). Sites were selected based on the presence of environmental indicators of *H. whipplei* habitat, such as serpentine soil, rocky outcrops, coastal sage-chaparral scrub plant communities (Gucker 2012), and if the blooming inflorescence density was high enough to provide plants along several transects. Each site included three 30 m transects that were randomly assigned either a treatment of exposure to a gradient of direct artificial night lighting ("light-treated") or no exposure ("control"). In total, we designated eight light-treated transects and seven control transects. Light towers marked the beginning of each transect and consisted of two solar powered spotlights (DINHAND, 54 led, 400 lumen, blue-white spectra with 448nm peak wavelength; see Supplementary material Appendix 1 Methods and Fig. A2) attached to a 3-m pole (Fig. 1). Direct light-treated transects provided artificial light from dusk until dawn every night of the experiment. The direction of each light-treated transect was designed to ensure emitted light did not shine in the direction of any other transects within the same site. Additionally, transects were located at least 100 m (mean = 137.7 m,  $\pm 31.3$  m) from each other to maintain independence, as the range of adult yucca moths do not typically exceed 50 m (Marr et al. 2000). Although located at approximately the same elevation to minimize variation in abiotic conditions, transects were separated by undulating topography that shielded the viewscape from one transect and area within approximately 30 m from others in the same site.

Along each transect we selected yucca plants at four distances from the light towers: 1 m, 3 m, 9 m, and 30 m (Fig. 1). Distances were chosen to represent the inverse square law of light attenuation, resulting in 4 orders of magnitude difference in light levels along the transects. Because flowering yucca plants did not always occur at our predetermined distances, we selected the closest flowering plant to each point and measured actual distances to the light source for each. Yucca plants were monitored once a month to assess the progress of blooming yucca stalks until the fruit were fully developed, which lasted from April through August 2019. Ideally, this design would have resulted in four plants per transect for a total of 60 plants; however, two of the selected plants at the 1-m mark did not produce inflorescence due to herbivory. Consequently, these plants were dropped from the final analysis, resulting in a total of 58 plants for our analysis of fruit set.

### *Light measurements*

Measurements were taken on nights of similar conditions between May 23rd to June 14th. All light measurements were taken after astronomical twilight had started when the sun was at least 12° below the horizon. To only capture light conditions produced by ALAN, measurements were taken when the moon was positioned below the horizon. Ideally, measurements should be taken under cloudless conditions to ensure additional diffuse irradiance does not interfere with the readings. However, the marine fog layer was always present during measurements, so these values report conditions yucca plants and moths typically experience during the flowering season.

Due to the differences in light properties between direct and indirect lighting (henceforth ‘direct light’ and ‘skyglow’, respectively), we used separate instruments to measure the two types of ALAN. Direct light from the treatment towers was measured with a handheld light meter (Minolta-T10a, Konica Minolta Sensing Americas, Inc) in units of lux, which is an illuminance value relative to human vision (Seymoure et al. 2019b). Recognizing that moths and many other organisms have spectral sensitivities different from humans, we also measured the radiance of the light sources (see supplemental methods). To measure the amount of direct light from the treatment towers reaching the sample plants, we oriented



the light meter directly towards the light tower at approximately the same height as the base of the inflorescence. To account for slight variation in the measurement readings, we took the mean of three separate measurements and used this value for subsequent analyses.

We measured indirect artificial light from skyglow using a Sky Quality Meter- Lens (SQM-L) device (Unihendron). The SQM-L is a hand-held device that incorporates a lens for collecting light from a narrow field of view that is approximately 20 degrees wide, specifically for city use where surrounding lights or buildings may affect the reading. Skyglow values were recorded as magnitudes/ arcsecond<sup>2</sup> (mpsas), which report inverse brightness in magnitudes spread out over a square arcsecond of the sky. We measured skyglow at each sampled plant along the transects by holding the SQM-L directly towards the zenith and recorded six measurements. We discarded the first measurement to calibrate the device, and we averaged the remaining five measurements for subsequent analyses. Furthermore, because skyglow would not systematically vary within each transect, we averaged the measurements at the 3 m, 9 m, and 30 m plants per transect, but excluded those at the 1 m plants because the angle from the SQM-L at that location would have detected light emitted by the treatment lights. Because the mpsas scale is logarithmic, relative, and reversed, we converted skyglow values to candelas (cd/m<sup>2</sup>) using  $10.8 \times 10^4 \times 10^{(-0.4 * (\text{mpsas}))}$ . Finally, we confirmed measurements did not systematically differ between direct light-treated and control transects (two-sample t-test,  $t = 0.239$ ,  $p = 0.815$ ) or between astronomical and true night measurements (two-sample t-test,  $t = -1.861$ ,  $p = 0.079$ ).

An important distinction is that although lux and candelas are both values representing light intensity, lux represents illuminance (i.e. the amount of light striking a surface) whereas candelas represent luminance (i.e. the emitted light from a specific cone in space), and thus the two measurements are not directly relatable. However, when comparing between zenith luminance in candelas and illuminance in lux, one can estimate one from the other by a factor of  $2\pi$  (see Kocifaj et al. 2014).

### *Environmental variables*

To control for biotic variation among sites, we used circular plots within a radius of 7.5 m (176.6 m<sup>2</sup> area) of each selected yucca plant and counted the total number of yucca rosettes, number of plants that were blooming, and the number of dead inflorescence stalks. For plants at the 1- and 3-m locations, densities were calculated from areas that overlapped with the arc of emitted light and distance from the treatment towers (sampled areas of 100.1 m<sup>2</sup> and 123.7 m<sup>2</sup>, respectively). These variables are indicative of potential moth recruitment, as moth larvae from previous years will emerge from underneath plants with senesced stalks and will travel to nearby blooming plants to lay their eggs (Aker and Udovic 1981). Therefore, the density of flowering yucca from previous seasons, as well as the number of blooms in near proximity, are important covariates that could influence the number of adult moths interacting with plants in our transects. Finally, using the geographic coordinates of each plant, we measured elevation (meters), slope (percent), and aspect (degrees) in ArcGIS (ESRI 2011).

#### *Adult moth abundance*

We deployed a separate set of light towers during the peak of yucca flowering to assess whether adult moths responded to the direct light treatment with phototaxis. Four light towers were installed at a sixth site (Supplementary material Appendix 1 Fig. A1) independently located from the towers used in the fruit set and larva recruitment experiment. These towers were deployed for seven days (May 10-17) with two control towers and two light treatment towers that were at least 100 m apart. At approximately an hour before sunset (17:00- 18:00) we attached two dual-sided 15.24 cm x 20.32 cm yellow adhesive sticky traps (GIDEAL, Inc.) to the poles to collect flying invertebrates, specifically moths. At approximately an hour after sunrise the next morning (7:00-8:00) we collected the sticky traps, quantified the number of yucca moths and other arthropods trapped (henceforth ‘abundance’), and switched the treatment for each tower (i.e. control became treatment and vice versa). This process repeated each night for seven nights. Additionally, the density of blooming yucca and dead stalks were counted within a 15-m radius (706.9 m<sup>2</sup>) to account for site variation and potential deviations in the density of emerging adult yucca moths.

### *Yucca plant and yucca moth recruitment*

To regulate the resources that sustain both growing fruit and the yucca larvae inside them, yucca plants will selectively abort pollinated flowers and fruit. Yuccas only produce fruit from 10% of all flowers, and this high abortion rate is often a result of hyper-oviposition, leading to larval crowding in fruit and increased larval mortality (James et al. 1994). Fruits are then more likely to abort if they are damaged or have fewer seeds, late to be initiated, or cross-pollinated from another plant species (James et al. 1994). Once the yucca plants aborted excess flowers and the pollinated fruits matured, we counted the total number of fruit for each plant as a metric of recruitment (henceforth “fruit set”). Previous studies have shown that the number of yucca fruits produced is an excellent predictor of seed set and therefore plant recruitment (Aker and Udovic 1981). For moth recruitment, we collected fruit from sampled plants (which ranged from 1 to no more than 5), dissected the fruit within 24 hours of collection, and counted the number of moth larvae per fruit as a metric of moth recruitment. Plants that did not produce fruit were dropped from the larval analyses, resulting in a total of 42 plants and 191 fruit.

### *Analyses*

We used program R (R Core Team 2019) for all analyses. We used generalized linear mixed models (GLMMs) with Poisson error for all models with packages *lme4* and *MASS*. Preliminary analysis revealed a slight overdispersion for models explaining fruit set and adult moth abundance, yet the *testZeroInflation* function in the *DHARMA* package revealed no evidence of zero inflation in the dataset. As such, we included an observation-level random effect (OLRE) to provide each data point a unique level of a random effect (Harrison 2014). For the adult moth abundance models, we also included light tower ID to account for site variation as a random effect. In preliminary recruitment analyses, to account for the hierarchical sampling design we constructed models with a nested random effects structure of site,

transect ID, and plant ID for fruit set and larva count. However, we removed random effects from the model structure when the resulting fits were singular or when the estimated variance was zero (Bates et al. 2015). Thus, both fruit set and larva models had the nested random effects of transect ID and plant ID and fruit set also had the OLRE.

In addition to the random effects, both moth abundance and arthropod abundance models included treatment (light-treated or control), bloom density, and dead stalk density as fixed effects. The biotic variables were used to account for additional site variation. Model selection (see below) with reduced parameters did not improve model performance (Supplementary material Appendix 1 Table A1). To avoid overfitting recruitment models, we first used two sets of candidate models to assess the influence of abiotic or biotic environmental variables on mature fruit set and larva counts before including light measurements. Abiotic variables include elevation, slope, and aspect. Biotic variables include yucca rosette density, blooming inflorescence density, dead stalk density, and mature fruit set counts for the larval models. All fixed effects were centered and scaled to facilitate direct comparison of their effects. We ranked all combinations of the abiotic or biotic environmental variables using AIC with the package *MuMIn*. For each set, variables whose effect sizes were within a model with  $\Delta AIC \leq 2$  and with 85% confidence intervals (CI) that did not overlap zero were included in subsequent light models that addressed our hypotheses (Supplementary material Appendix 1 Tables A2, A4, A6, and A8 for ranked models of biotic fruit, abiotic fruit, biotic larval, and abiotic larval variables).

We constructed two light models to explicitly test our predictions for the influence of light exposure on fruit set and larva count. The first model tested for a treatment effect (light-treated vs control) to identify if the presence of direct artificial light elicited changes in recruitment for these species (henceforth “treatment” models). The second model tested for a relationship between the light intensity emitted by the treatment towers and fruit set or larva count (henceforth “illuminance” models). The treatment and illuminance models also included an interaction term with skyglow. Variables in the light models were assessed by ranking models by AIC and we report the compiled list of top performing models. We concluded that there was evidence that variables within models in the competitive set

( $\Delta AIC \leq 2$ ) had an influence on the response if the variable's confidence interval did not overlap zero, which is a common use for evaluating effects in information theoretics (Arnold 2010). Specifically, we report 95% CIs to reflect higher precision of estimates and 85% CIs for others that warrant consideration for inference. Finally, because the modeling effort and data inspection suggested that nonlinear functions may also explain the relationships between direct light or skyglow and fruit set and larva count, and because responses to environmental drivers are commonly nonlinear in ecology and evolution (Kreyling et al. 2018), we considered second order polynomial functions of logarithmically scaled light values in a *post hoc* analysis. We compared these models and assessed the influence of parameter estimates as described above to determine whether the polynomial function improved model fit over the linear relationships in strongly supported models. However, for all recruitment models, the inclusion of a second order polynomial term did not improve model performance (not shown), and we present all results with linear relationships.

## Results

### *Adult moth abundance*

The presence of direct artificial light strongly increased the mean counts of arthropods ( $\beta = 0.887$ ; 85% CI: 0.240, 1.515) and yucca moths ( $\beta = 3.183$ ; 95% CI: 1.553, 6.091) caught on traps relative to control conditions (Fig. 2).

### *Light and yucca fruit*

All light models pertaining to mature fruit set were assessed with skyglow and a variable representing direct light because no additional abiotic or biotic environmental parameter had an influence on fruit set (Supplementary material Appendix 1 Tables A3 and A5). While treatment appeared in a competing model, it did not have a strong influence on fruit set. Illuminance models revealed a positive relationship between light exposure and mature fruit set ( $\beta = 0.326$ ; 85% CI: 0.019, 0.657; Table 1; Fig. 3). Across all light models, skyglow consistently appeared in the top ranked model and resulted in an

increase in mature fruit set ( $\beta = 1.033$ ; 95% CI: 0.185, 2.037). Strongly supported intensity models also included an interaction between direct light and skyglow; however, confidence in the effect size was low.

### *Light and the yucca moth*

All larval light models were assessed with yucca rosette density, blooming inflorescence density, and aspect (Supplementary material Appendix 1 Tables A7 and A9, respectively). For all models, larva count was strongly influenced by aspect ( $\beta = -0.230$ ; 85% CI: -0.439, -0.0510; Table 2), as conditions favored plants on hills facing North and East. Yucca rosette density also appeared in competing models ( $\beta = 0.215$ ; 85% CI: 0.000, 0.400). Additionally, a portion of competing models included density of blooming inflorescence, but this variable did not have a strong influence on larva count.

While illuminance levels appeared in a competing model, it did not elicit a strong effect, suggesting larva counts did not vary with the presence or across the gradient of direct light. Matching the positive association between mature fruit set and skyglow, an increase in skyglow was associated with an increase in larva counts ( $\beta = 0.184$ ; 85% CI: 0.008, 0.382; Table 2; Fig. 4). However, this is weak evidence for impacting moth recruitment, as the null model was also included with the competitive set.

## **Discussion**

Light pollution created by ALAN is increasingly recognized as a major driver of nocturnal insect declines (Knop et al. 2017, Owens et al. 2020), yet little research has investigated the effects or mechanisms behind diurnal pollinator response to this anthropogenic stimulus. Here, we provide evidence that suggests a diurnal yucca moth exhibits positive phototaxis to artificial night lighting. Moreover, we only caught one moth across all trials under dark conditions, and all trap locations received both light and dark conditions, thus serving as their own controls, which provided additional confidence in this observed response. Plants exposed to direct artificial light produced higher fruit set. Because *H. whipplei* is self-incompatible (Powell and Mackie 1966), an increase in fruit set implies an increase in pollination, which purportedly occurs after oviposition (Aker and Udovic 1981). Despite resulting in increased plant fruit

set, direct light did not elicit a reciprocal change in larva counts, suggesting there are other mechanisms influencing moth reproduction and recruitment, such as physiological damage or misdirected behaviors. Furthermore, both plants and moths experienced an increase in recruitment under brighter light polluted areas, suggesting the ambient skyglow provides more opportunities for moths to pollinate and oviposit. The presence of ALAN most likely influences adult moth behavior and other factors that contribute to reproductive output, for unlike other moth species, yucca larvae develop inside an enclosed fruit pod (Baker 1986) and are thus shielded from ALAN.

### *Direct light*

Fruit counts increased with increasing light intensity, suggesting that moth behavior follows the concentration hypothesis (Macgregor et al. 2015), such that they are attracted and disperse towards plants closer to light sources and end up pollinating a greater number of flowers for these individuals. While treatment did not have an influence on fruit counts, light intensity did, which suggests a certain threshold of light exposure must be met before diurnal moths become attracted and move toward the light source. Since the yucca moth in our study is diurnal and thus regularly experiences light intensities many orders of magnitude greater than those in our treatments, it is possible that increased light levels do not elicit ancillary adult pollination behavior.

Although the described sequence of pollination following oviposition would suggest that larva recruitment should match the pattern of increased fruit set with direct light exposure, we found no difference in larval recruitment between lit and unlit sites, and no relationship with direct light levels. The unaffected larva count also implies that sources of direct light do not indirectly influence moth recruitment via changes in the host plant, as more fruit pods would indicate an increased availability of protected enclosures during development and increased seed set as food resources (Aker and Udovic 1981). There are no clear explanations for the mismatch in the effect of direct light on yucca fruit set and yucca moth larva counts. One possibility is artificial lighting that exceeds natural nighttime conditions could elicit adverse physiological consequences or misdirected behaviors. Indeed, several aspects of moth

reproduction have been recorded to change when exposed to ALAN, such as inhibiting female sex pheromone release, inducing male sterility, and disrupting female oviposition (Owens and Lewis 2018). Still, evidence from other diurnal insects, such as *Drosophila melanogaster*, suggests that even exposure to dim ALAN levels (i.e. ~1 lux) can disrupt oviposition and lead to fewer eggs laid (McLay et al. 2017), suggesting that the mere presence of ALAN can alter fitness-relevant behaviors. This could explain why pollination is successful, but oviposition did not reciprocally increase, as moths are able to carry out reproductive activities during the day with full visual capabilities, yet their reproductive capabilities may become hindered by excessive light exposure. Moreover, our adult moth abundance results provide unambiguous evidence that moths are attracted to lights at night, suggesting that the presence of ALAN might mislead moth activity to extend their temporal niche beyond daylight hours (Macgregor et al. 2015, Desouhant et al. 2019). Nevertheless, direct lights could interfere with the moth's visual system. Moths flying away from the light may be functionally blinded as the pigment within the eye expands in response to the stimulus (Hamdorf and Höglund 1981). If moths are engaging in nocturnal oviposition activity, there is the possibility that they are no longer able to discriminate between the stamen and pistil and are misdirected when they deposit eggs. Another example of misdirected activity was observed by Aker and Udovic (1981), as they described a behavior where female moths drew their tentacles across the stigma, searching for pollen, but made no attempt to oviposit. Misdirected behaviors could be amplified by the presence of ALAN, yet further research is needed to determine whether the decrease in moth recruitment is altered by mechanisms influencing physiology, behavior, or a combination of these factors.

#### *Ambient skyglow*

Skyglow increased yucca fruit set, suggesting that skyglow increases nocturnal pollination. We found mixed evidence that larva counts follow the same pattern, which may result in a weaker association with oviposition activity, but presumably not pollination activity. Skyglow increases background brightness up to three orders of magnitude above natural nighttime conditions (Seymoure et al. 2019a) and can result in ambient lighting of up to 0.15 lux in wilderness areas near cities (Gaston et al. 2013,



Seymoure et al. 2019a). This intensity could be bright enough to alter the perceived photoperiod (Macgregor et al. 2015, Desouhant et al. 2019). The probability of moth activity extending into the night will depend on peak flight activity, as diel activity is not strictly confined to daylight hours and varies by species (Lamarre et al. 2015). While diurnal insect sensitivity to wavelengths have been described for several species (see Donners et al. 2018), sensitivities to light intensity is relatively unknown, such as the threshold of artificial light that misleads diurnal insects into extending their temporal activities into the night and potentially inciting phototaxis. Even without knowing the specificities of moth visual sensitivity, the degree to which ALAN influences nocturnal oviposition can be determined by the yucca moth's natural photoperiodic entrainment. For example, when exposed to varying daylight hours, the ovipositional rhythm of the diurnal *Culex tarsalis* was reciprocally altered to oviposit bimodally during the first few hours of the photophase and again at the beginning of the scotophase, alluding to ovipositional behavior controlled by entrainment to light intensity changes (Beck 1980). If yucca moths entrain to oviposit with variation in light levels in a similar way, extension of light duration could alter their ability to properly entrain for oviposition. Furthermore, increased exposure to ALAN might alter metabolic processes. Melatonin is not only responsible for endogenous patterns such as enhanced cell maintenance and mitochondrial activity, but it also is a major driver of biological rhythm and daily activities (Jones et al. 2015). While *T. maculata maculata* only survives as an adult for a few days, the extended temporal activity could have dire consequences on longer lived species, as long-term exposure to stress can lead to compromised immune responses, regulation of metabolism, and decreased reproductive output (Desouhant et al. 2019). Conversely, female yucca moths have finite energy reserves, and the combination between increased metabolic work when exposed to artificial nightlight and allocating energy to dispersal and egg production could contribute to decreased moth recruitment.

#### *Plant response to ALAN*

Changes in adult moth behavior and / or physiology are the most likely explanation for changes in plant and moth recruitment; however, the possibility exists that plants respond directly to variation in

direct and indirect light. Plants interact with light via photosynthesis mechanisms, yet the light produced by skyglow is typically thought to be inadequate to elicit a sufficient response on carbon fixation, and ultimately should not alter the physiology or resource allocation to fruit set (Bennie et al. 2016).

However, some yucca species are thought to be resource-limited rather than pollinator-limited. For example, a study on *Yucca elata* mature fruit set showed that regardless of yucca moth abundance or hand-pollination of flowers on inflorescences, plants did not alter mature fruit set and aborted ninety percent of moth-pollinated flowers (James et al. 1994). Whether this is the case in *H. whipplei* is not known. Thus, while we would not expect skyglow to change the availability of resources that typically limit plant reproductive success (i.e., phosphorus and available nitrogen), we cannot eliminate the possibility that skyglow could influence energy availability and thus the support of more mature fruit.

Finally, the positive relationship between skyglow and fruit set could be the result of timing. For example, several studies have reported plant blooms occur earlier seasonally with the presence of light pollution (French-Constant et al. 2016, Singhal et al. 2019). Earlier blooms could favor plant reproduction by coinciding with lower temperatures and greater soil water availability. This temporal shift may be optimal for *H. whipplei*, which relies most heavily on seasonal rainfall patterns for producing and sustaining large inflorescences (Baker 1986). Consequently, an advanced flowering season elicited by skyglow could also indirectly influence yucca moth emergence and recruitment, as the timing of emergence is closely synchronized with flowering (Powell and Mackie, 1966). However, yucca moth flight activity may be limited by lower ambient temperatures (Addicott et al. 1990), which could limit the adult moths' ability to cross-pollinate yucca individuals and oviposit in diverse flower ovaries.

Unfortunately, we have a limited ability to explore these possibilities because our study lacked the temporal resolution to determine whether plants exposed to skyglow or direct light bloomed earlier. Future studies should compare the timing of yucca blooms under the presence of varying levels of skyglow to see if ambient light pollution advances or delays flowering, and consequently, if moth emergence and pollination activity follow suit.

## Conclusion

While studies have investigated the potential outcomes of exposure to ALAN for nocturnal populations (Wilson et al. 2018, Desouhant et al. 2019, Owens et al. 2020), we provide evidence that ALAN causes a diurnal pollinator to be active at night and that the fitness of its obligate host appears to increase with both direct and indirect ALAN. If and whether other diurnal pollinators also experience positive phototaxis will be important foci for future studies, as will whether ALAN influences the physiology, behavior, or multiple factors relating to reproduction and fitness of both plants and pollinators. Regardless, given that growth in ALAN is outpacing global population growth (Kyba et al. 2017), our results suggest that a greater understanding of how this novel selection pressure influences a variety of plant-pollinator communities is vital.

## Declaration

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**Author contributions** – AAW, BMS, and CDF conceived of the experiment and secured funding. AAW, SJ, RV, BM, LP, and HP collected data. AAW conducted most data analysis with contributions from BMS and CDF. AAW wrote the original draft of the manuscript and received feedback from all authors.

**Conflicts of interest** – We report no conflicts of interest.

**Data availability statement** – The data underlying this article are available in its online supplementary material.



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## FIGURE CAPTIONS

Figure 1. Treatment tower set up for each of the fifteen transects at our study sites (A). Experimental design of transects and yucca placement from the treatment towers (B). Yucca plants are selected at approximately 1 m, 3 m, 9 m, and 30 m from the light towers, and plants are exposed to direct artificial light in the designated light-treated transects, as shown with approximate illuminance values (lux).

Figure 2. Bar plots representing (A) the distribution of total arthropods (control  $n = 165$ , light  $n = 551$ ) and (B) adult yucca moths (control  $n = 1$ , light  $n = 22$ ) caught on insect traps per trial.

Figure 3. Estimated effect sizes of fruit set counts when exposed to increasing (A) illuminance levels (lux) and (B) skyglow (candelas) with points representing empirical counts and bands representing the 85% and 95% confidence level interval, respectively, around the estimated effect size. Independently, both direct light and skyglow cause plants to increase mature fruit set production.

Figure 4. Estimated skyglow effect on larval count per fruit across all sites. Points represent empirical counts, and bands represent the 85% confidence level interval around the estimated effect size. High levels of skyglow saw an increase in larval counts across all sites.

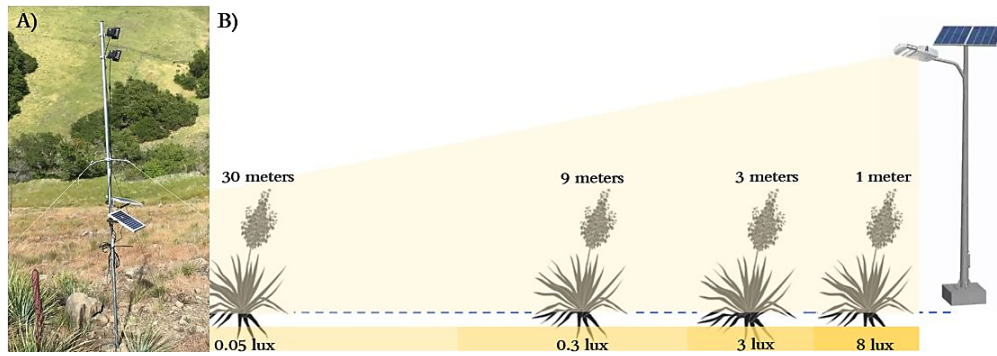


Figure 1. Treatment tower set up for each of the fifteen transects at our study sites (A). Experimental design of transects and yucca placement from the treatment towers (B). Yucca plants are selected at approximately 1 m, 3 m, 9 m, and 30 m from the light towers, and plants are exposed to direct artificial light in the designated light-treated transects, as shown with approximate illuminance values (lux).

94x32mm (300 x 300 DPI)

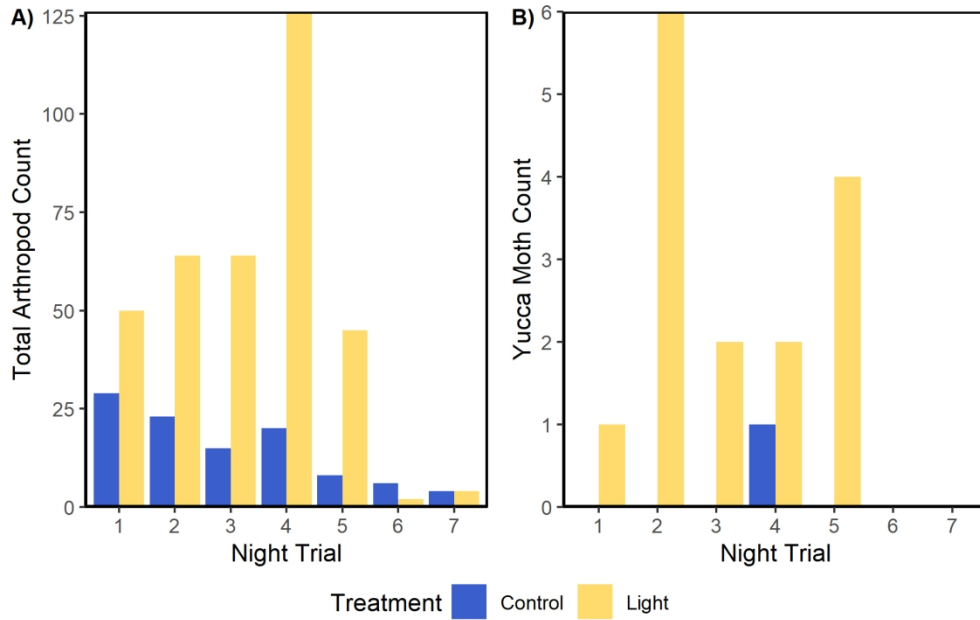


Figure 2. Bar plots representing (A) the distribution of total arthropods (control n = 165, light n = 551) and (B) adult yucca moths (control n = 1, light n = 22) caught on insect traps per trial.

159x99mm (300 x 300 DPI)

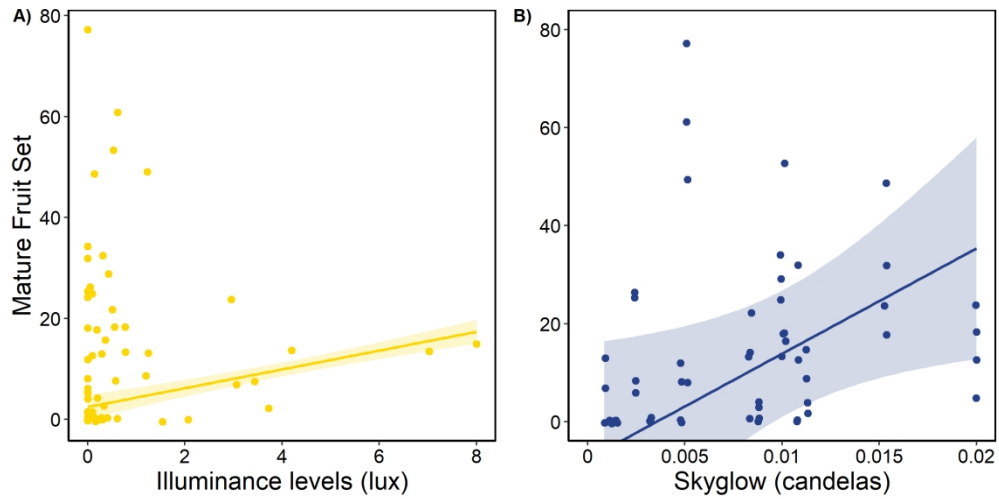


Figure 3. Estimated effect sizes of fruit set counts when exposed to increasing (A) illuminance levels (lux) and (B) skyglow (candelas) with points representing empirical counts and bands representing the 85% and 95% confidence level interval, respectively, around the estimated effect size. Independently, both direct light and skyglow cause plants to increase mature fruit set production.

239x119mm (300 x 300 DPI)

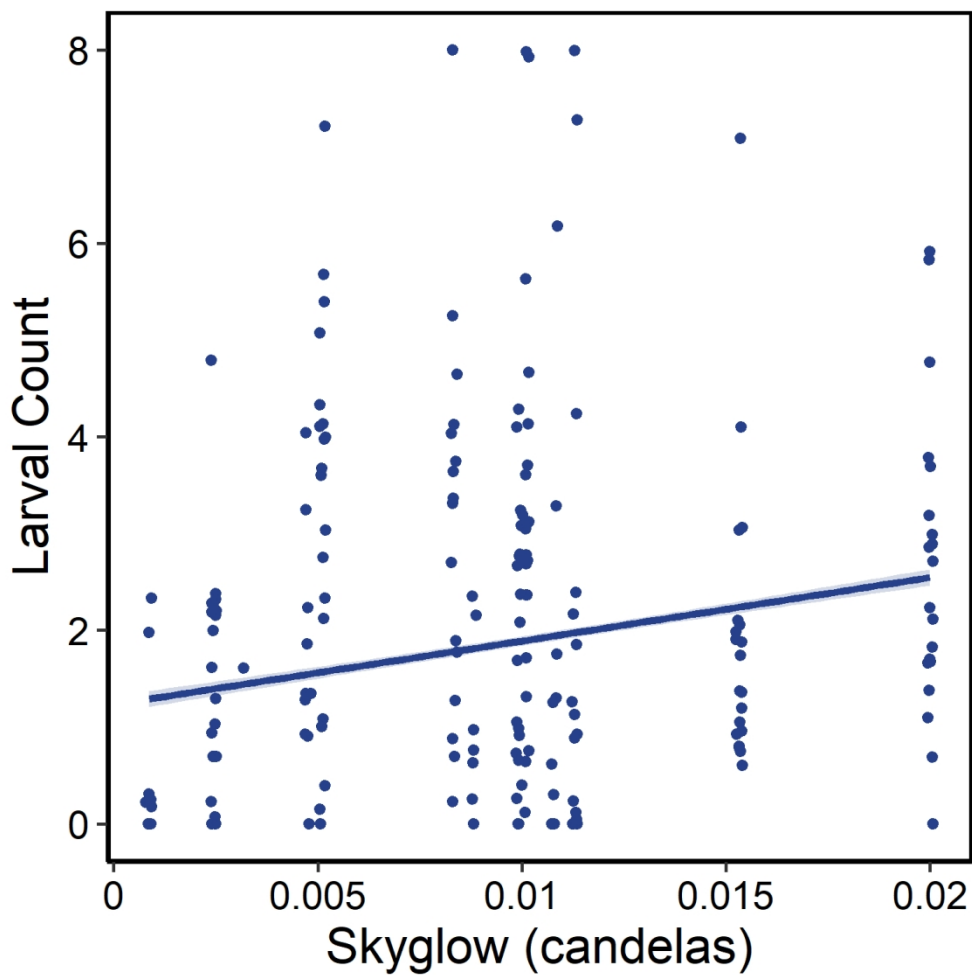


Figure 4. Estimated skyglow effect on larval count per fruit across all sites. Points represent empirical counts, and bands represent the 85% confidence level interval around the estimated effect size. High levels of skyglow saw an increase in larval counts across all sites.

99x99mm (400 x 400 DPI)

Table 1. Model selection table of all models for the treatment and illuminance effects on mature fruit set, in addition to the null model (intercept only). All models include transect ID and plant ID as nested random effects.  $K$  indicates the total number of parameters in the model and weight corresponds to competing models within 2.00  $\Delta AIC$ . Model parameters included in the global model are Skyglow, Treatment (light-treated or control), direct light intensity emitted from the treatment towers (Illuminance), the interaction between skyglow and treatment (Skyglow\*Treatment), and the interaction between skyglow and illuminance levels (Skyglow\*Illuminance). Bolded variable names indicate predictors with 85% confidence intervals that do not overlap zero.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i><math>\Delta AIC</math></i>	<i>weight</i>
<b>Skyglow</b>	4	401.4	0.00	0.38
<b>Skyglow</b> + Illuminance	5	402.1	0.72	0.27
<b>Skyglow</b> + Treatment	5	402.8	1.45	0.19
<b>Skyglow</b> + <b>Illuminance</b> + Skyglow*Illuminance	6	403.0	1.65	0.17
Null	3	404.8	3.43	--

Table 2. Model selection table of all models for the treatment and illuminance effects on moth larva counts, in addition to the null model (intercept only). All models include transect ID and plant ID as nested random effects.  $K$  indicates the total number of parameters in the model and weight corresponds to competing models within 2.00  $\Delta AIC$ . Light model parameters included in the global model are Skyglow, Treatment (light-treated or control), direct light intensity emitted from the treatment towers (Illuminance), the interaction between skyglow and treatment (Skyglow\*Treatment), and the interaction between skyglow and illuminance (Skyglow\*Illuminance). Environmental variables tested are yucca rosette density (Density), blooming inflorescence density (Blooms), and Aspect. Bolded variable names indicate predictors with 85% confidence intervals that do not overlap zero.

<i>Model</i>	<i>K</i>	<i>AIC</i>	<i><math>\Delta AIC</math></i>	<i>weight</i>
<b>Aspect</b>	4	694.9	0.00	0.22
<b>Aspect</b> + Skyglow	5	696.0	1.08	0.13
<b>Skyglow</b>	4	696.1	1.24	0.12
<b>Aspect</b> + Density	5	696.2	1.25	0.12
Null	3	696.4	1.50	0.10
<b>Aspect</b> + Treatment	5	696.8	1.87	0.084
<b>Aspect</b> + <b>Density</b> + Blooms	6	696.8	1.87	0.084
<b>Aspect</b> + Blooms	5	696.9	1.95	0.081
<b>Aspect</b> + Illuminance	5	696.9	2.00	0.079