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Effects of Low-Level Artificial Light at Night on Kentucky Bluegrass and Introduced Herbivore

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7
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25 **Abstract**

26 Increasing evidence suggests that artificial light at night (ALAN) can negatively impact
27 organisms. However, most studies examine the impacts of ALAN on a single species or under high
28 levels of artificial light that are infrequent or unrealistic in urban environments. We currently have
29 little information on how low levels of artificial light emanating from urban skyglow affect plants
30 and their interactions with herbivores. We examined how low levels of ALAN affect grass and
31 insects, including growth rate, photosynthesis, and stomatal conductance in grass, and foraging
32 behavior and survival in crickets. We compared growth and leaf-level gas exchange of Kentucky
33 Bluegrass (*Poa pratensis*) under low-levels of ALAN (0.3 lux) and starlight conditions (night light at
34 0.001 lux). Furthermore, each light treatment was divided into treatments with and without house
35 crickets (*Acheta domesticus*). Without crickets present, bluegrass grown under artificial light at night
36 for three weeks grew taller than plants grown under natural night light levels. Once crickets were
37 introduced at the end of week three, grass height decreased resulting in no measurable effects of light
38 treatment. There were no measurable differences in grass physiology among treatments. Our results
39 indicate that low levels of light resulting from skyglow affect plant growth initially. However, with
40 herbivory, ALAN effects on grass may be inconsequential. Gaining an understanding of how ALAN
41 effects plant-insect interactions is critical to predicting ecological and evolutionary consequences of
42 anthropogenic disturbance.

43 1 Introduction

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44 Artificial light at night (ALAN) is an anthropogenic pollutant that is increasing spatially by a
45 rate of 2.2% per year (Kyba et al., 2017). Direct ALAN sources, such as streetlights, can lead to
46 skyglow: the atmospheric scattered light that can propagate up to several hundred kilometers into the
47 environment (Aubé, 2015; Luginbuhl et al., 2009; Aubé, 2015). Skyglow results in light encroaching
48 into natural areas where direct sources of light pollution are not present (Gaston et al., 2015; Garrett
49 et al., 2020). The study of artificial light at night as an anthropogenic pollutant is a relatively young
50 field (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021), with
51 most studies conducted at relatively high levels of nocturnal light pollution (e.g., 10-100 lux; (Gaston
52 et al., 2013) but see (Alaasam et al., 2018; Sanders and Gaston, 2018). These high light levels are
53 representative of organisms functioning under direct light pollution, such as directly beneath a
54 streetlight, whereas most urban environments exist at lower light levels due to skyglow (e.g., 0.1 to 1
55 lux), which can impact environments several hundred kilometers away from a direct light source
56 (Gaston et al., 2013; Dominoni et al., 2014; Seymoure et al., 2019a). For reference, a full moon night
57 could create ambient light levels of 0.3 lux on its brightest nights (Biberman et al., 1966; Kyba et al.,
58 2017). Therefore, examining the impacts of light pollution at high intensities, although informative,
59 is not representative of artificial light conditions in urban habitats at night. It remains an open
60 question as to whether low levels of skyglow illumination (0.001 lux - 0.3 lux) affects communities
61 to the same extent as direct illumination.

62 The intensity and spectral composition of light depends upon the phase of the moon, season,
63 and weather, all of which create necessary cues for organisms (Kyba et al., 2015; Spitschan et al.,
64 2016; Seymoure et al., 2019b). Plants use light as a cue for almost every physiological process
65 including, but not limited to, seedling development, photosynthesis, growth, and budding (Takemiya
66 et al., 2005; Bennie et al., 2016; Gaston et al., 2017; Singhal et al., 2018). Light influences plant
67 growth, development, and photosynthetic efficiency (Briggs and Christie, 2002). In addition to
68 powering the electron transport chain in thylakoid membranes, light intensity and direction increases
69 photosynthetic efficiency through phototropism (i.e. the movement of the plant towards sunlight;
70 (Celaya and Liscum, 2005), chloroplast movement (Wada et al., 2003), and light-induced stomatal
71 opening to help optimize gas exchange efficiency (Dietrich et al., 2001). Periods of darkness are also
72 important for plant metabolic processes, particularly stress recovery, which includes recovery from
73 herbivory events (McNaughton, 1983; Singhal et al., 2018).

74 Increased levels of ALAN from urbanization are changing natural light regimes by increasing
75 the intensity and duration of light available at night (Davies et al., 2013; Seymoure et al., 2019a;
76 Buxton et al., 2020), potentially affecting plant photosynthesis, growth, and plant-herbivore
77 interactions. For example, by masking natural night light levels, ALAN can mislead herbivores to be
78 more active at night and disrupt plant-herbivore interactions and critical dark recovery periods for
79 plants (Dominoni et al., 2020). Plants in light polluted environments experience changes in
80 pollination, photoreceptor signaling, phenology and flowering (Ffrench-Constant et al., 2016; Singhal
81 et al., 2018), which can have ecological consequences for food web dynamics (Polis et al., 2004).
82 However, little is known about how constant illumination at the level of urban light alters plant-insect
83 interactions. ALAN has led to declines in population sizes of a diversity of insect species through its
84 interference with insect development, movement, foraging, and reproductive success, which can alter
85 trophic systems (Owens and Lewis, 2018; Owens et al., 2020).

86 Here we test whether ALAN affects plant-insect interactions by modifying plant
87 photobiology and growth rates. We exposed two common urban species—Kentucky bluegrass (*Poa*
88 *pratensis*), a cool season common turfgrass (Weissman et al., 1977; Suplick-Ploense and Qian, 2005;
89 Read et al., 1999; Weissman et al., 1977; Suplick-Ploense and Qian, 2005), and the house cricket

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90 (*Acheta domesticus*), a nocturnal herbivore—to starlight (0.001 lux) and realistic urban night light
91 levels (0.3 lux) (Dominoni et al., 2013; Alaasam et al., 2018; Seymoure et al., 2019a) in order to test
92 the following hypotheses: 1) Low levels of ALAN affect plant physiology. We predicted that plants
93 grown under urban light would have higher net photosynthesis and dark respiration, increased growth
94 rates, and increased stomatal conductance compared to control plants grown under starlight
95 conditions. 2) Herbivory interacts with ALAN to affect plant biomass. We predicted cricket
96 herbivores would reduce the biomass and height of grass. However, as crickets are nocturnal
97 foragers, we predicted they would consume less plant material under urban light than starlight
98 conditions and have lower survival rates in urban light.

99 ## 2 Materials and Methods

100 ### *2.1 Light Treatments*

101 We used a CMP6050 growth chamber (Version 4.06, Conviron, Winnipeg, Manitoba) set to a
102 temperature of 22.2°C with light control to create artificial light environments (0.3 lux, hereafter
103 “urban light”) and natural new moon light environments (0.001 lux, hereafter “starlight”)(Dominoni
104 et al., 2013; Alaasam et al., 2018; Seymoure et al., 2019a; Jones et al., 2020). There were two
105 different light types in the chamber - high pressure sodium and mercury vapor - placed in alternating
106 positions on the ceiling of the chamber. To create urban light levels within the chamber, we used 4
107 layers of filter gels over the light sources (Rosco E-Colour #211 .9 Neutral Density Filter, Stamford,
108 CT) that attenuated 83% of light. To further attenuate light, 90% black shade cloth was placed over
109 starlight treatments, and 22% white shade cloth was placed over urban light environments. These
110 were constructed as square boxes and placed over the plant treatment groups using PVC pipe and
111 shade cloth. We confirmed that light levels were approximately 0.3 lux and 0.001 lux using a highly
112 sensitive spectroradiometer (StellarNet Silver Nova, Tampa Bay, FL) with a cosine corrected
113 irradiance probe affixed to a 1000-micron optical fiber (StellarNet, Tampa Bay, FL). We checked
114 irradiance measurements using SpectraWhiz software (StellarNet, Tampa Bay, FL); due to the low
115 light levels, we set integration time to approximately 20 seconds for the 0.3 lux measurements and 8
116 minutes for the 0.001 lux measurements. This confirmed that light levels throughout the enclosure
117 were within one order of magnitude of the chosen light level for each treatment: 0.3 and 0.001 lux.

118 ### *2.2 Experimental Design*

119 On day 1, Kentucky bluegrass seeds were sown in 10 cm round pots (n=72) containing Scotts
120 Miracle-Gro soil and placed in the growth chamber under experimental light conditions. On day 21,
121 we measured the tallest blade of grass, then weeded down the pots randomly until there were 25
122 shoots of grass remaining. After the initial 21-day growth period, one randomly selected juvenile
123 cricket, male or female, was placed in each of 36 designated cricket pots. Herbivory and light
124 environments were examined using a 2x2 factorial design in which light treatment was factorially
125 crossed with cricket treatment in a 28-day experiment. The four treatments were arranged in a block
126 test pattern, as shown in **Figure 1**. Treatment groups included: (1) plants without crickets in urban
127 light, (2) plants without crickets in starlight, (3) plants with crickets in urban light, and (4) plants with
128 crickets in starlight (n=18 per treatment). Nighttime lighting conditions were imposed in the middle
129 of the day from start of the experiment to ensure nighttime measurements could be taken during
130 regular working hours. Lighting conditions were altered twice daily; we placed filter paper and shade
131 cloth structures over the plants at 08:00 and removed them at 18:00 to create a 14:10 light: dark cycle
132 typical of summer in the northern hemisphere. Blocks were rotated daily one position clockwise to
133 account for spatial variation in light levels within the chamber, and generously watered at this time.

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134 Drierite (W.A. Hammond 23005, Xenia, OH) was placed in two trays on opposite sides of the
135 chamber to control humidity and prevent mold growth (Hammond, 1935).

136 Crickets were sourced as juveniles from a stock population from Premium Crickets (Winder,
137 Georgia) in December 2018 and May 2019 at the mean size of 1.9 centimeters, before adult morph.
138 From day 21 to 28, cricket survival was monitored daily (i.e., when light conditions were shifted) and
139 categorized as alive or dead. If a cricket was found dead, the cricket and its designated plant were
140 removed from the experiment. Upon removal, we measured the height of the tallest blade of grass
141 and recorded the length of time the plant/cricket spent in the chamber. We also cut and weighed
142 above ground biomass to determine wet and dry mass. On day 28, we removed all remaining plants
143 from the experiment and recorded the final height of the tallest blade of grass. We calculated the
144 average daily growth rate in week four (day 21 to day 28) to control for plants that were removed
145 prematurely due to cricket death.

146 ### *2.3 Gas Exchange Measurements*

147 To assess light treatment effects on bluegrass physiology independent of herbivory, we
148 measured leaf photosynthetic responses on day 19 before crickets were placed into pots. We
149 measured leaf gas exchange in each light treatment using a LI-6400XT infrared gas analyzer with a
150 leaf chamber fluorometer attached (Li-Cor Biosciences; Lincoln, NE) following previously published
151 methods with slight modifications (Lemoine et al., 2018). Plants were removed from the growth
152 chamber temporarily for gas exchange measurements. The environmental conditions inside the leaf
153 chamber were standardized across measurements; leaf temperature was maintained at 20°C, relative
154 humidity was maintained between 40-50%, sample chamber flow rate was set to 200 µmol s^{-1}, and
155 reference chamber CO_2 concentration was set to 400 ppm. Low flow settings are commonly used for
156 small leaved grasses with low photosynthetic rates (Taylor, 2014). Leaf level gas exchange was
157 measured under two light conditions: dark and low light (10 µmol m^2 s^{-1} (740 lx) photosynthetically
158 active radiation; PAR). Gas exchange in the dark provides an estimation of leaf respiration. The low
159 light level was the minimum amount of light provided by the Li-6400 light source; thus, we were
160 unable to measure photosynthesis under the tested ALAN conditions imposed here (<10 umols, <740
161 lux), but instead measured whether treatments had an impact on plant photosynthetic responses to
162 low levels of light. Results are reported in regard to light treatment in the growth chamber (urban
163 light or starlight). A newly emerged and fully expanded leaf from each individual (n= 10 individuals
164 per treatment) was inserted into the leaf chamber. Prior to measurements, leaves were dark adapted
165 for 2 hours under a dark box that allowed no light to enter. Leaves were left in the chamber for 2-5
166 minutes to equilibrate to chamber conditions before gas exchange parameters (photosynthesis or
167 respiration, and stomatal conductance) were recorded (average of three logged values taken in rapid
168 succession). Steady-state fluorescence (Fs) was measured continuously before exposing plants to a
169 saturating pulse of light (2750 µmol m^{-2} s^{-1} of blue light or ~203,500 lux (Thimijan and Heins, 1983)
170 to measure maximum chlorophyll fluorescence. Light inside the chamber was then switched to the
171 low light level (10 µmol m^2 s^{-1}). Once gas exchange reached stability, net photosynthetic rate, and
172 stomatal conductance were recorded, and a saturating pulse was applied to estimate photosystem II
173 efficiency (ΦPSII): $\Phi PSII = (Fm' - Fs)/Fm'$ where Fm' represents chlorophyll fluorescence under
174 low light. As grass blades rarely fill the entire chamber, the measured leaf area was estimated using
175 width and length, and photosynthetic parameters, which are based on the area of the chamber (6 cm^2),
176 were adjusted accordingly.

177 ### *2.4 Data Analysis*

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178 All statistical analyses were performed in R version 3.4.3(R Development Core Team, 1999).
179 We first confirmed the use of parametric tests to ensure our data was normally distributed. To test our
180 first hypothesis that gas exchange increased under ALAN, we ran a MANOVA with net
181 photosynthetic rate, stomatal conductance, dark respiration, and ΦPSII as response variables and with
182 light treatment and block as explanatory variables (**Figure 2**). For our second hypothesis that light
183 and cricket treatments would affect plant height, we modeled daily percent change in height between
184 day 21 and day 28 using a two-way ANOVA with light treatment, cricket treatment, and block as
185 explanatory variables (**Figure 3**). We then analyzed the data using two-way ANOVA, again with
186 light treatment, cricket treatment, and block as explanatory variables. We tested for an interaction
187 between light treatment and cricket treatment, and we also analyzed cricket survival using Kaplan-
188 Meier analysis with the "survival" package in R (**Figure 4**) (Therneau and Lumley, 2009).

189 3 Results

190 There was no difference in net photosynthesis, stomatal conductance, dark respiration, or ΦPSII
191 between grass grown in the two light treatments (**Table 1**). On day 21, bluegrass grown in urban light
192 was taller (mean = 6.58cm, sd = 2.3) than bluegrass grown in starlight (mean = 7.10cm, sd = 2.67,
193 **Table 2**). However, daily percent change in plant height from day 21 to day 28 was not significantly
194 different (**Table 3**). The presence of crickets did affect plant height, whereby bluegrass with crickets
195 present were shorter than bluegrass without crickets (**Table 3**).
196 Crickets in the urban light treatment had a 25.0% probability of survival, whereas crickets in the
197 starlight treatment had a survival probability of 32.1%, but this difference was not significant
198 (Kaplan-Meier: n = 36, p = 0.37, see supplemental material). There was no difference in survival due
199 to sex (Kaplan-Meier: n= 36, p= 0.80, see supplemental material).

200 4 Discussion

201 Our study explored how low levels of artificial light at night, which are widespread across
202 ecosystems, may affect plants and plant-insect interactions. Contrary to our predictions, grass grown
203 under urban light conditions after 19 days did not have higher net photosynthetic rates than those
204 grown under starlight, nor did stomatal conductance, dark respiration, or ΦPSII differ significantly
205 between light treatments. However, plants under urban light conditions grew taller than plants grown
206 under starlight conditions during the initial 21 days of growth before crickets were introduced.
207 Additionally, we found no evidence that crickets under urban light consumed more plant matter than
208 crickets in starlight treatments, and survival rates of crickets did not differ between treatments. The
209 results from this study suggest that low levels of ALAN may not have significant effects on grass
210 photobiology but may affect plant height.

211 Studies investigating grass responses to higher levels of illumination (e.g., 4±1 µmol?m-2?s-1
212 or 296 lux) found that plant photoreceptors were damaged causing changes to flowering phenology
213 (Thimijan and Heins, 1983; Shin et al., 2010; Bennie et al., 2016). The lower levels of light tested
214 here were likely not bright enough to induce these changes in bluegrass. Plants often use nighttime
215 darkness to repair damage from UV rays, suggesting the low levels of ALAN in our treatments may
216 be dark enough for plants to continue to repair damaged cells and photoreceptors (Singhal et al.,
217 2018). Moreover, net photosynthesis is a dynamic measurement that can vary within samples due to
218 time and day(Miller et al., 1996) and our single measurement at the end of week 3 may not have
219 captured treatment differences occurring at other times.

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220 We found no difference in stomatal conductance or respiration between plants grown in urban
221 light and starlight. Other studies have noted differences in stomatal density and stomatal opening and
222 closing in the presence of ALAN (Takemiya et al., 2005; Shimazaki et al., 2007). Another study
223 found that yellow-poplar trees exposed to ALAN (high pressure sodium lighting ranging from 82 lx
224 to 4100 lx) for three years resulted in reduced nighttime stomatal conductance (Kwak et al., 2018). It
225 is possible that our light levels were too low, or grass was not subjected to our light levels for a long
226 enough duration to induce such responses. Reduced chlorophyll and rubisco concentration has been
227 observed in phytoplankton grown under low light levels (6.6 lux;(Poulin et al., 2014), and light as
228 low as 3.5 lux has induced flowering in tree species across the United Kingdom (Ffrench-Constant et
229 al., 2016). We also observed no treatment effects on photosystem II efficiency despite other studies
230 noting adverse reactions in these physiological responses to light pollution (Zhang and Reisner, 2019;
231 Meravi and Prajapati, 2020). Kentucky Bluegrass might be more adaptable to changing light regimes
232 given that it is commonly used as a turf grass selected for its resilience to drought and heat stress
233 (Wang and Huang, 2004). We observed a faster growth rate for grasses grown under urban light
234 conditions compared to starlight conditions. Plant growth rate is determined by a variety of factors,
235 including, but not limited to, photosynthetic rate, specific leaf area, leaf mass fraction, and nitrogen
236 absorption rate(Poorter et al., 1991; Osone et al., 2008). Although we found no difference in net
237 photosynthetic rate between treatments, growth rate differences could have been due to greater
238 allocation to leaf area in urban light(Poorter and Remkes, 1990), although we did not measure such
239 attributes.

240 ALAN is known to alter photoperiod detection in multiple organisms (Bennie et al., 2016)
241 and these changes in photoperiod can impact plant growth and flowering (Cathey and Campbell,
242 1975; Blanchard and Runkle, 2010; Basler and Körner, 2012; Craig and Runkle, 2016). Increased
243 growth and biomass have been noted in *Poaceae* species when exposed to high levels of ALAN
244 ranging from 0.349 - 1.145μmols m^2 sec^{-1} from metal halide bulbs (Flowers and Gibson, 2018),
245 which is approximately 24.78 - 81.30 lux (Thimijan and Heins, 1983). Since we noted no change in
246 Kentucky Bluegrass, photoperiod detection may not have been disrupted at our lower levels of
247 ALAN, or it may have caused undetectable or non-measured physiological responses.

248 While animals rely on plants as a food source and shelter, we found no evidence that low-
249 level light pollution would impact these typical interactions between plants and insects. Artificial
250 light at the level of 0.3 lux was not significant enough to mask natural light cues in herbivores, nor
251 mislead herbivores in foraging behaviors, but light pollution at higher levels could modify these
252 interactions(Gaston et al., 2013; Macgregor et al., 2015; Bennie et al., 2016; Knop et al., 2017). High
253 levels of ALAN could mask lunar cues, disrupting invertebrate behavior and feeding patterns and
254 could attract invertebrates to artificially lit structures, deterring them from normal behavioral patterns
255 (Longcore and Rich, 2004; Seymoure, 2018; Dominoni et al., 2020; Sanders et al., 2021).

256 Overall, our research detected few changes to plant physiology at low levels of urban light,
257 suggesting that low levels of ALAN may not be as harmful to community interactions as predicted.
258 Other studies conducted at high levels of ALAN suggest artificial light can induce large changes in
259 physiology and community interactions(Longcore and Rich, 2004; Gaston et al., 2013; Seymoure et
260 al., 2019a). There may be a threshold level at which artificial light becomes harmful, causing
261 detrimental effects to individual and ecosystem function with additional increases in intensity and
262 duration. Understanding and identifying this threshold would allow for more effective management
263 of night skies and natural light conditions(Dominoni et al., 2020). With estimates suggesting two
264 thirds of Key Biodiversity Areas experience ALAN(Seymoure et al., 2019a; Garrett et al., 2020), it is

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265 important to identify the level at which artificial light becomes harmful and how natural night skies
266 can be managed.

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276 *The authors declare that the research was conducted in the absence of any commercial or financial*
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278

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439 **Table 1** MANOVA table of the gas exchange results evaluating differences in photosynthesis,
440 stomatal conductance in dark, stomatal conductance in light, fluorescence, and photosystem II
441 efficiency.

	df	Pillai	*f*	*p*
Treatment	**1**	**0.18**	**0.45**	**0.83**
Block	**3**	**0.95**	**1.09**	**0.40**
Residuals	**17**			

442

443 **Table 2** ANOVA table comparing mean grass height at day 21 across light treatments and blocks. *
444 indicates a significant response.

	Sum of Squares	*df*	Mean Square	F	*p*
Light Treatment	**3.50**	**1**	**3.50**	**5.63**	**0.021***
Block	**7.87**	**6**	**1.31**	**2.11**	**0.064**
Residuals	**39.8**	**64**	**0.622**		

445

446 **Table 3** ANOVA table showing the effects of light treatment, cricket treatment, and block (plus
447 interactions between light and cricket treatment and cricket and block treatment) on daily percent
448 change in grass height between day 21 and the end of the experiment. * indicates a significant
449 response.

	Sum of Squares	*df*	Mean Square	F	*p*
Light Treatment	**0.14**	**1**	**0.14**	**1.60**	**0.21**
Cricket Treatment	**2.82**	**1**	**2.82**	**32.04**	**5.3×10^{-7}***
Block	**0.85**	**6**	**0.14**	**1.62**	**0.16**
Light: Cricket	**0.002**	**1**	**0.002**	**0.023**	**0.88**
Cricket: Block	**0.90**	**6**	**0.15**	**1.70**	**0.14**
Residuals	**4.93**	**56**	**0.088**		

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453 **Figure 1:** Aerial view of treatment groups in the growth chamber after crickets were introduced (day
454 21-28). The treatment groups were arranged in a block test pattern with 4 blocks of urban light
455 treatments and 4 blocks of starlight treatments, totaling 8 groups (A-H). Within each block (A-H),
456 nine plants (every other one) had a cricket.

457 **Figure 2:** **(A)** Net photosynthesis across light treatments, measured under low light conditions (10
458 μmols m^{-2} s^{-1} of light) and **(B)** stomatal conductance across light treatments. **(C)** Photosystem II
459 efficiency is measured using a saturating pulse (ΦPSII): ΦPSII = (Fm′ − Fs)/Fm’ where Fm is
460 chlorophyll fluorescence under low light. **(D)** Dark respiration measured under low light level (<10
461 μmols m^{-2} s^{-1} of light). There were no differences in net photosynthesis, stomatal conductance,
462 Photosystem II efficiency, or dark respiration between light treatments.

463 **Figure 3:** **(A)** Bluegrass height at day 21 separated by light treatment when no crickets were present.
464 Grass in urban light was taller than grass in starlight conditions. **(B)** Daily percent change in height of
465 grass (change from day 21 to day 28 divided by the number of days in the chamber) separated by
466 light treatment. There was no difference in daily percent change across light or cricket treatments.

467 **Figure 4:** Survival probability of crickets. **(A)** Survival probability of crickets under urban light and
468 starlight treatments. **(B)** Survival probability of crickets under urban light and starlight treatments,
469 split by sex in each treatment group. In all both comparisons **(A-B)**, there were no differences in
470 survival.

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