Effects of artificial light at night on the foraging behavior of an endangered nocturnal mammal[☆]

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ABSTRACT

Modification of nighttime light levels by artificial illumination (artificial light at night; ALAN) is a rapidly increasing form of human disturbance that affects natural environments worldwide. Light in natural environments influences a variety of physiological and ecological processes directly and indirectly and, as a result, the effects of light pollution on species, communities and ecosystems are emerging as significant. Small prey species may be particularly susceptible to ALAN as it makes them more conspicuous and thus more vulnerable to predation by visually oriented predators. Understanding the effects of disturbance like ALAN is especially important for threatened or endangered species as impacts have the potential to impede recovery, but due to low population numbers inherent to at-risk species, disturbance is rarely studied. The endangered Stephens' kangaroo rat (SKR), *Dipodomys stephensi*, is a nocturnal rodent threatened by habitat destruction from urban expansion. The degree to which ALAN impacts their recovery is unknown. In this study, we examined the effects of ALAN on SKR foraging decisions across a gradient of light intensity for two types of ALAN, flood and bug lights (756 vs 300 lumen, respectfully) during full and new moon conditions. We found that ALAN decreased probability of resource patch depletion compared to controls. Moreover, lunar illumination, distance from the light source and light type interacted to alter SKR foraging. Under the new moon, SKR were consistently more likely to deplete patches under control conditions, but there was an increasing probability of patch depletion with distance from the source of artificial light. The full moon dampened SKR foraging activity and the effect of artificial lights. Our study underscores that ALAN reduces habitat suitability, and raises the possibility that ALAN may impede the recovery of at-risk nocturnal rodents.

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1. Introduction

The addition of artificial illumination into natural environments at night (artificial light at night; ALAN) is a rapidly expanding form of human disturbance. Recent analyses of night sky brightness indicate that 23% of the Earth's non-polar land surface is exposed to ALAN and 80% of the world population experiences significantly brightened night skies (Cinzano et al., 2001; Falchi et al., 2016). ALAN generally increases with human population growth (Bennie et al., 2015), but in recent years has risen more dramatically in some countries, such as the United States (Falchi et al., 2019). As one of the brightest countries, over half the United States experiences light polluted nights (Falchi et al., 2016; Kyba et al., 2017).

While astronomers have called for policies to limit ALAN for over four decades (Riegel, 1973), more recently, there has been a surge of interest in elucidating the impacts of ALAN on ecological systems. Natural light directly and indirectly affects how animals interact with their biotic and abiotic environment. Given how important natural light is for regulating activity patterns (Foster and Kreitzmann, 2004; Grant et al., 2013; Prugh and Golden, 2014), navigation during migration (Akesson et al., 2001), nocturnal predator-prey dynamics (Buchanan, 1993; Lima, 1998; Prugh and Golden, 2014), and communication with conspecifics (Branham and Wenzel, 2003; Endler, 1993), it is not surprising that research shows significant impacts of light pollution on wildlife in variety of ways (Delhey and Peters, 2017; Gaston et al., 2015; Hölker

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et al., 2010; Longcore and Rich, 2004). For instance, artificial light can affect physiological processes by altering the immune response (e.g. hamsters; Bedrosian et al., 2013; Bedrosian et al., 2011), stimulating production of stress hormones (great tits; Ouyang et al., 2015) and shifting the circadian rhythm and thus reproductive period (blackbirds; Dominoni et al., 2013; lemurs; LeTallec et al., 2015; wallabies; Robert et al., 2015). Behaviorally, ALAN has been shown to influence movement patterns by misorienting, attracting or deterring animals (e.g. moths; Frank, 2006; petrels; Le Corre et al., 2002; sea turtles; Rivas et al., 2015), altering courtship and/ or mate choice (e.g. field crickets; Botha et al., 2017; songbirds; Kempenaers et al., 2010; fruit flies; McLay et al., 2018), and foraging activity (e.g. frugivorous bats; Lewanzik and Voigt, 2014; shorebirds; Santos et al., 2010). There are even documented effects at the ecological and ecosystem levels. For example, artificial light can reduce food sources (e.g. aphids; Bennie et al., 2015), disrupt pollination services (e.g. nocturnal insect pollinators; Knop et al., 2017), shift community composition (e.g. ground dwelling invertebrates; Davies et al., 2012), and may affect carbon turnover (e.g. photoautotrophs; Hölker et al., 2015). The effects of artificial light have been shown to impact every major taxonomic group, but are particularly important to evaluate for nocturnal species.

A large portion of mammals are active primarily at night (Jones et al., 2009), and ALAN is very likely to affect them (Duffy et al., 2015) given that mammalian evolution was likely driven by adaptations for nighttime activity (Heesy and Hall, 2010). Nocturnal mammals experience natural fluctuations in ambient light levels associated with monthly lunar cycles. Under natural full moon conditions, nocturnal small rodents show decreased above-ground activity and forage under dense cover rather than in open areas (Blair, 1943; Clarke, 1983; Daly et al., 1992; Kaufman and Kaufman, 1982; Kotier et al., 2010; Kotler, 1984; Lockard and Owings, 1974; Travers et al., 1988). It has long been thought that these energetically costly behavioral changes are a response to increased predation risk (Lima and Dill, 1990), and this was confirmed by a recent meta-analysis (Prugh and Golden, 2014). By contrast, there is relatively little research on the impacts of artificial light on small rodents; a few studies have shown it can affect their above-ground activity and foraging decisions. For example, the endangered coastal nocturnal Florida beach mouse (*Peromyscus polionotus leucocephalus*) reduces patch use and foraging frequency in response to artificial lighting (Bird et al., 2004), nocturnal Patagonian leaf-eared mice (*Phyllotis Xanthopygus*) decrease above-ground activity under high ALAN conditions (Kramer and Birney, 2001) and cathemeral bank vole (*Myodes glareolus*) populations alter space use (Hoffmann et al., 2018).

Understanding impacts of disturbance like ALAN is likely to be especially important for threatened or endangered species. Management of at-risk species relies on understanding factors that affect fitness and viability, in order to identify and preserve or restore habitat suitable for species recovery (Sutherland et al., 2009; Sutherland et al., 2004). Habitat suitability modeling is an effective tool used to help managers identify the most promising locations to support recovery of threatened or endangered species (Mateo-Tomas and Olea, 2010; Millspaugh et al., 2009). ALAN and other human activities characteristic of the highly modified environments of the Anthropocene are starting to be included in evaluations of species distributions (Ciach and Frohlich, 2017, 2019; Froidevaux et al., 2017), but to date, have not been included in habitat suitability models. It is critical that we develop a more comprehensive understanding of these types of human-mediated impacts in order to effectively manage and recover these species.

Here we present the first in a series of experiments that examines the effects of ALAN on endangered rodents in the family Heteromyidae (kangaroo rats, kangaroo mice and pocket mice). In this study, we test the hypothesis that artificial light in natural habitat impacts the foraging decisions of the endangered Stephens' kangaroo rat, *Dipodomys stephensi* (SKR). We predicted that SKR would reduce foraging activity when exposed to artificial illumination, that SKR foraging would increase with distance from the light source and that higher intensity lighting would have a larger effect on resource patch depletion than low-intensity lighting. With 31 species of rodents listed as threatened or endangered in the U.S. alone (USFWS, 2019) and many more on the decline (Ceballos et al., 2015; Pimm et al., 2014; Schipper et al., 2008), it is more important than ever to understand how anthropogenic elements such as light may limit their recovery.

2. Material and methods

2.1. Study species

The SKR is a medium-sized nocturnal granivorous rodent in the family Heteromyidae that is native to flat open grasslands and sparse coastal sage scrub in Riverside and San Diego counties, California (U.S.A.) (Price et al., 1994a; USFWS, 1997). Similar to other heteromyids (Brown and Heske, 1990), it is considered a keystone species because its seed-caching and soil disturbance activities significantly alter plant community structure (Brock and Kelt, 2004; Goldingay et al., 1997). SKR are prey to diverse taxa, including bobcats (*Lynx rufus*), coyotes (*Canis latrans*), rattlesnakes (*Crotalus* spp.), foxes (*Vulpes* spp.), weasles (*Mustela* spp.), and owls (*Tytonidae* and *Strigidae*). Since 1970, habitat fragmentation and loss of habitat to agriculture and suburban development have been the most direct causes of decline of SKR (Price and Endo, 1989). The species was listed as threatened under the California Endangered Species Act in 1971 because a substantial amount of habitat throughout its range had been lost. In 1988, the U.S. Fish and Wildlife Service classified Stephens' kangaroo rat as endangered under the U.S. Endangered Species Act. The range of SKR continues to decline as a direct result of habitat destruction for development and agriculture purposes (Roach, 2018).

2.2. Study site

We conducted experiments for this study on the Southwestern Riverside County Multispecies Reserve in southern California (33° N, 117° W, mean elevation 472 m) in 2012 and 2014. The study site was a plateau of open temperate grassland that had been previously managed with mowing and a prescribed fire to provide appropriate SKR habitat. The study site was located away from human activity and therefore this SKR population had no prior exposure to direct ALAN. No other small rodents were documented on the site during trapping surveys associated with other projects, but desert cottontails (*Sylvilagus audubonii*) were present on site and have been observed to consume seed bait at small rodent traps (Shier, unpublished), despite their primarily herbivorous diet (Flinders and Crawford, 1977).

2.3. Light arrays and treatments

In early summer 2012, we established 20 linear arrays of ten experimental resource patches 5 m apart. At the end of each array, we installed a metal pole (3 m) with an artificial light mounted at the top to create a light gradient. SKR are territorial and maintain small home ranges (0.05−0.2 ha) with home range cores averaging only 30 m (Price et al., 1994b; USFWS, 1997). Therefore, arrays were set at least 50 m apart to ensure independence with respect to the group of SKR that were likely to visit foraging patches within an array and reduce the chance of light from one treatment array

affecting another array. We tested SKR response to three light treatments: 1) flood light (high intensity), 2) bug light (low intensity) and 3) control (new moon light) (Fig. 1). For the flood light treatment, we used a SolarGoesGreen Super Bright Solar Flood Light, 108 light-emitting diode (LED; 150-Watt incandescent equivalent) which emitted high intensity light 756 lm at wavelengths between 400 and 700 nm (see Supplementary Fig. 1(a) for spectrum). The bug light treatment was a yellow hue Feit Electric 13-Watt Compact Fluorescent (60-Watt incandescent equivalent) bulb, which emitted low intensity light (300 lm) at wavelengths between 550 and 650 nm (see Supplementary Fig. 1(b) for spectrum) and was housed in an aluminum clamp light surround. Each night we randomly assigned each array to one of the three light treatments, and each light treatment was implemented at each array over a 3-night period. We collected data within 3 d of a new moon to standardize natural illumination. We replicated this experiment in 2014 with 12 arrays but used full moon light as the control treatment.

At a representative array with the light turned on, we averaged three light measurements at each experimental resource patch (Fig. 2; Supplementary Table 1). We measured light intensity with a SILVER-Nova Super Range (190−1110 nm) TE Cooled Si-CCD linear array based Spectroradiometer with a miniature UV-Vis-NIR cosine receptor calibrated for irradiance to NIST traceable calibration lamps and SpectraWiz Spectrometer Software v. 5.33 (StellarNet, Inc.). We used a tripod to hold the sensor facing the light source eight cm off the ground where light measurements reflect the amount of illumination a SKR would experience. We measured vector irradiance ($\mu W/cm^2$) rather than lux, as lux measurements are weighted according to human visual spectral sensitivity (Johnsen, 2012). We then converted light measurements to nmol photons/s/m^2 according to (LABRIGGER) using the peak wavelength of each light source and to lux using 555 nm as the middle of the visible light spectrum, with (UnitConverter) to allow for
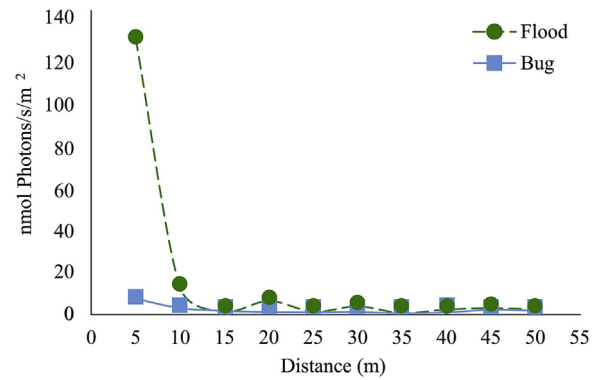

Fig. 2. Mean light irradiance nmol photons/s/m^2 at resource patches in a representative array under a bug light (blue solid) or a flood light (green dashed) in response to distance (m) from light source. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

comparison to other studies. All measurements were taken on the same night under a clear sky and at least 2 h after sunset and 2 h before sunrise.

2.4. Resource patches

Each array contained 10 resource patches, each consisting of a recycled cardboard tray set flush with the ground and filled with sieved site soil. We pre-baited trays with approximately 5−10 g of millet each night for one week prior to experiments to ensure resource patches were discovered by the kangaroo rats. During experiments, we placed 12.5 g of sterilized millet seed in a pile along the center of each tray. Approximately 30 m before dawn, all trays were collected. We used the presence of fresh cottontail feces on trays to determine if cottontail visitation affected patch
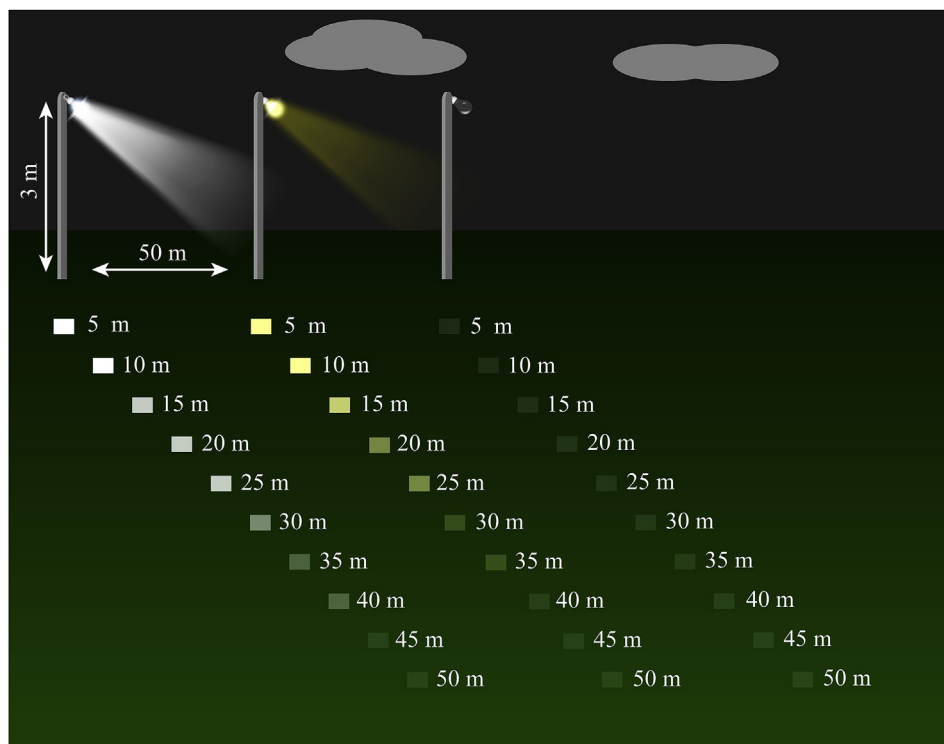

Fig. 1. Experimental Design. Graphic of experimental design showing 3 light treatment arrays (flood, bug and control) and associated microhabitat patches arrays.

depletion and included the presence or absence of cottontails as a covariate in the analysis (see Data analysis section below). After collection, each tray was sifted for remaining seed. We oven-dried collected seed at 65 °C for 30 m and weighed the seed to determine how much seed remained in each tray.

2.5. SKR density

We used burrow counts to estimate the density of SKR in the vicinity of the linear arrays. We conducted 5×50 m belt transects by scanning each array to a distance of 2.5 m on either side of the center line. While burrow numbers are not directly correlated with SKR numbers, burrow entrances serve as a good index of SKR abundance (O'Farrell, 1992).

2.6. Data analysis

For the majority of resource patches, SKR either took nearly all of the seed in the patch or left all of the seed. Therefore, we classified foraging as a binomial variable. Resource patches with less than 0.0125 g of seed remaining were categorized as depleted, and resource patches with more than 0.0125 g of seed remaining were categorized as not depleted. We used logistic regression models to evaluate the likelihood of SKR depleting resource patches in response to the following predictor variables: light treatment, distance from the light source, moon condition (new or full), SKR density (burrows) and all potential interaction terms. We allowed for intra-group correlation and clustered by array to account for repeated measures on arrays since each array was used for all three light treatments. We used Akaike information criterion (AIC) to evaluate model fit and quantified the relative impact of factors on foraging with log likelihood. We conducted Holm-Sidak post hoc pairwise tests to evaluate light treatment differences from each other and account for multiple comparisons. Because data on cottontail presence or absence was not taken for all resource patches and thus model comparisons with and without cottontails could not be made, we evaluated the effect of cottontails on resource patch depletion using a separate logistic regression model.

Data analysis was conducted with Stata/IC 14.2 (StataCorp, 2015). Data figures were made in JMP 13.1.0 (SASInstitute, 2019).

3. Results

Original data of this study are available at Mendeley Data https://doi.org/10.17632/g29z3rdbc6.1.

The full model that included all possible predictor variables was the top ranked model and model weights indicated no other candidate models were supported (Supplementary Material Table 2). Artificial light significantly altered foraging activity (Logistic Regression: Light treatment DF = 2, $\chi^2 = 19.59$, p < 0.01). Depletion of resource patches was significantly greater under the control light treatment than under illumination from flood lights (Holm-Sidak corrected pairwise comparison: z = −4.03, p < 0.01) and the bug light (Holm-Sidak corrected pairwise comparison: z = −2.70, p < 0.01). However, resource patch depletion did not differ significantly between bug and flood light treatments (Holm-Sidak corrected pairwise comparison: z = −1.46, p = 0.37).

While, when considered alone, there was no effect of distance from the light source or moon condition on SKR foraging activity (Logistic regression: distance: z = 1.15, p = 0.25; moon condition: $\chi^2 = 1.55$, p = 0.21), the likelihood of SKR depleting a foraging patch was related to the interaction between light treatment, distance from the light source and the moon condition (Logistic regression: light treatment x distance x moon condition: $\chi^2 = 6.76$, p < 0.03; Table 1; Fig. 3). Under illumination from the new moon, light

treatment and distance from the light source interacted to affect SKR foraging decisions ($\chi^2 = 9.82$, p < 0.01; Table 1, Fig. 3). For arrays under no artificial light (new moon control treatment), there was no difference in the probability of depleting a resource patch in response to increasing distance from the light source. Conversely, under both the bug and flood light treatments, the probability of SKR depleting a resource patch increased with distance from the light source. Under new moon conditions, impacts of low wattage bug lights on SKR foraging are significant to 40 m from the light source when compared to controls, while impacts of flood lights are significant to 50 m from the light source (Table 1).

In contrast, there was no significant interaction between light treatment and distance under the full moon condition ($\chi^2 = 0.23$, p < 0.89; Fig. 3). Under the full moon condition, SKR depleted foraging patches equally between the bug light and control conditions, and there was no difference in the probability of depleting a patch as a function of distance (Table 1). However, SKR were significantly less likely to deplete foraging patches under the flood light than under control light and the effect of the flood light under the full moon condition extended to foraging patches 40 m from the light source (Table 1).

SKR density in the vicinity of the arrays predicted foraging activity (Logistic Regression: burrows: z = 2.40, p < 0.02). Not surprisingly, SKR density was positively associated with an increased likelihood of resource patch depletion. The presence of cottontails did not affect patch depletion (Logistic Regression: z = −0.15, p = 0.88).

4. Discussion

Our findings are consistent with a growing body of research indicating that ALAN is a human-caused disturbance that impacts behavior of rodents that are active at night and is likely to have population-level consequences (Bird et al., 2004; Brown, 1988; Hoffmann et al., 2018; Kramer and Birney, 2001; Lockard, 1975). Our study demonstrates the disruptive effects of artificial light on SKR foraging energetics. In line with our prediction, SKR depleted fewer resource patches under ALAN compared to control patches. There was no significant difference in SKR patch depletion between the two artificial light treatments (flood and bug), although there was a trend indicating higher likelihood of patch depletion under illumination by the bug light than the flood light. While studies on other taxa have shown that lower intensity lighting is less disruptive to wildlife than higher intensity lighting (Longcore and Rich, 2004), and predict that yellow-green and amber emitting LEDs will have less impact than high-pressure sodium lamps (Longcore et al., 2018), our results show that similar to coast beach mice (Bird et al., 2004), even low-intensity yellow bug lighting significantly affects SKR energetics through alteration of their foraging decisions.

SKR likely avoid artificially lit foraging patches for a variety of reasons. Depending on the light intensity, they may simply avoid artificially lit areas because they are blinded when directly under the artificial light due to the physical properties of their eyes. SKR and other nocturnal mammals have large pupils and lenses, and retinas with many rods (Heesy and Hall, 2010). This structural combination allows extreme sensitivity to light but low acuity and can cause temporary blindness under bright light (Beier, 2006). In addition, similar to other prey species, SKR likely forage less when they are more visible to predators, and conditions are riskier (predation risk hypothesis; Mougeot and Bretagnolle, 2000). Results of a recent meta-analysis suggest that prey species that rely on visual communication and those that utilize habitat with higher levels of cover either benefit or are less impacted by higher natural light levels (Prugh and Golden, 2014). However, many nocturnal

Table 1
Distance of impact of light type and moon condition on Stephens' kangaroo rat foraging decisions in arrays 5−50 m from light source.

| Moon Condition	Bug Light			Flood Light		
	Distance (m)	z	p	Distance (m)	z	p
New	5	−5.28	0.000	5	−6.88	0.000
New	10	−5.25	0.000	10	−6.97	0.000
New	15	−5.15	0.000	15	−6.99	0.000
New	20	−5.00	0.000	20	−7.19	0.000
New	25	−4.72	0.000	25	−7.74	0.000
New	30	−4.13	0.000	30	−8.22	0.000
New	35	−3.18	0.001	35	−6.92	0.000
New	40	−2.07	0.038	40	−4.49	0.000
New	45	−1.07	0.284	45	−2.81	0.005
New	50	−0.30	0.763	50	−2.03	0.042
Full	5	−0.35	0.724	5	−2.07	0.038
Full	10	−0.44	0.663	10	−2.15	0.032
Full	15	−0.53	0.594	15	−2.21	0.027
Full	20	−0.65	0.517	20	−2.25	0.024
Full	25	−0.78	0.437	25	−2.27	0.023
Full	30	−0.92	0.360	30	−2.25	0.024
Full	35	−1.05	0.293	35	−2.19	0.029
Full	40	−1.16	0.246	40	−2.08	0.037
Full	45	−1.23	0.221	45	−1.93	0.053
Full	50	−1.24	0.214	50	−1.24	0.079
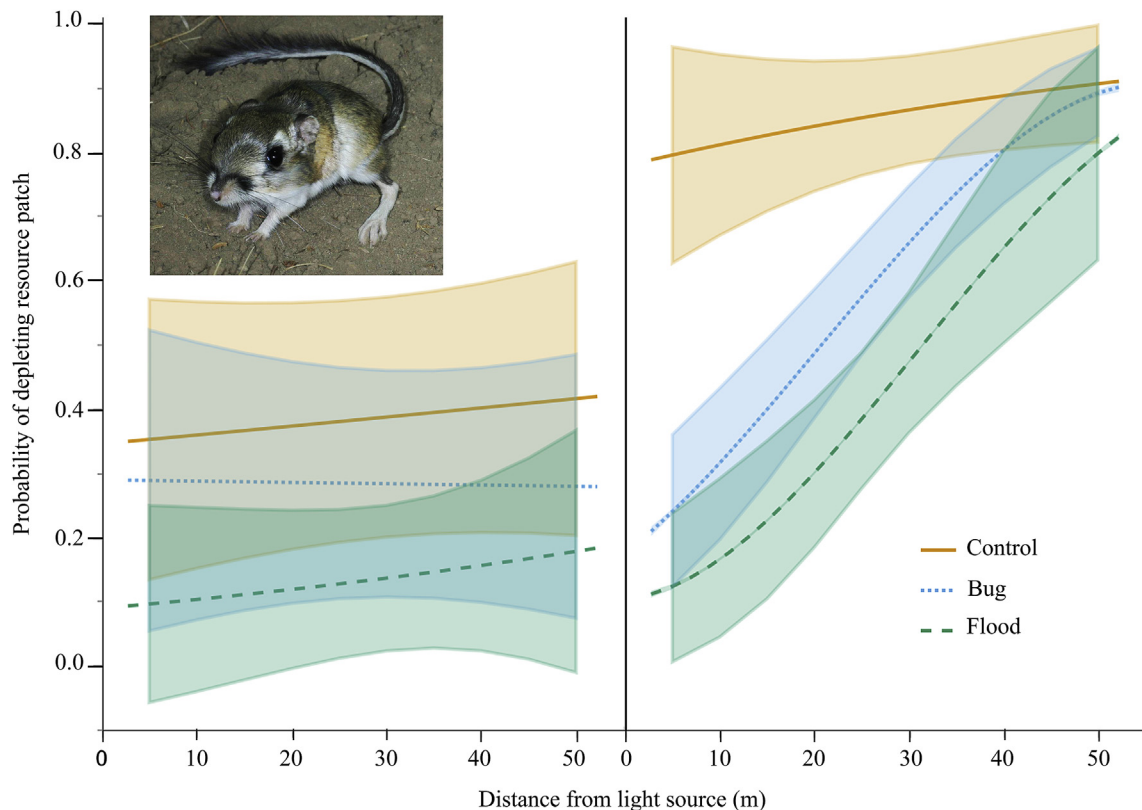
Fig. 3. Effect of light treatment (flood − green large dashed; bug − blue small dashed; control – orange solid) and distance (m) from light source under the full (left) or new (right) moon on probability of depleting a resource patch. The shaded areas show the 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

rodents like kangaroo rats rely on nonvisual forms of communication (olfactory and seismic; Randall, 1993, 1997; Randall et al., 2000; Shier et al., 2012; Shier and Yoerg, 1999). And, similar to effects of natural light, impacts of ALAN are likely greater for species with a preference for open habitat since such habitat provides little opportunity for dampening light impacts as a result of horizontal shading (i.e. the creation of discrete areas of darkness as a result of vegetation cover; Gaston et al., 2012). Indeed, research on Patagonian leaf-eared mice which forage in open habitat has shown that ALAN reduces above-ground activity (Kramer and Birney, 2001). Similarly, our results show that SKR, that exhibit strong open habitat preferences (Price et al., 1994a) are significantly impacted by artificial light.

The impact of artificial light on SKR foraging is mediated by

lunar illumination, distance from the light source and the light type. Under the new moon condition, the probability of patch depletion was the highest under the control treatment (no artificial light), with approximately 80–90% of foraging patches depleted regardless of distance along the array. By contrast, the probability that SKR would deplete a foraging patch increased quickly with distance from artificial light sources, indicating a decrease in impact of ALAN with distance from the source of artificial light. Light intensity from the bug and flood lights, as measured by vector irradiance, decreased with distance from the artificial light source up to 25 m, at which point light was no longer detected. Yet, our results showed significant effects of artificial lighting on SKR foraging up to 40 m from the bug light and 50 m from the flood light. Taken together these results suggest either that our spectrometer was not sensitive enough to measure the light greater than 25 m from the light source or that the effects of ALAN on SKR extend beyond the point at which light in the form of irradiance, is measurable. Similar to the response of black-tailed godwits (*Limosa*) to street lighting (De Molenaar et al., 2006), our results suggest that effects of sky glow on behavior may extend beyond those of irradiance, and highlight the need to measure both irradiance and radiance to understand the effects of ALAN on a species' behavioral ecology. Moreover, impacts of the flood light on SKR energetics may extend into habitat beyond 50 m from the light source as we found significant effects all way to the furthest patches. Impacts of ALAN on coastal beach mice foraging under vegetation cover were limited to 10 m from the light source (Bird et al., 2004), suggesting differential impact of ALAN in response to habitat preferences.

A different pattern emerged under the full moon condition. Not surprisingly, the full moon condition reduced SKR foraging across all light treatments with the lowest patch depletion under the highest light intensity (i.e. flood light treatment). The increased sky luminance from the full moon appeared to dampen the effect of the artificial lights, especially under the bug light treatment. SKR were equally likely to deplete foraging patches under the bug light and control conditions, regardless of distance from the light source. While the full moon also dampened the effect of the flood light, SKR patch depletion remained significantly different between the flood light and control condition up to 40 m from the light source. Thus, the full moon appeared to dampen the effect of the artificial lights, but the flood light was sufficiently bright to continue altering SKR foraging decisions. The flood light was brighter than the bug light, but also differed in spectral characteristics, shielding, and the amount of diffusion. The bug light was a compact florescent bulb emitting light in a narrow spectrum (550–650 nm), while the flood light was composed of several small white LED bulbs that emitted light at a broader spectrum of wavelengths (400–700 nm). Our experiment did not disentangle impacts of light intensity from spectrum. But, recent research shows that nocturnal rodent visual sensitivity peaks between 350-370 nm and 490–520 nm (de Farias Rocha et al., 2016) which overlapped with our flood lights, but was outside of the range wavelengths emitted by the bug light. This suggests that both intensity and spectral characteristics of the flood light may have contributed to the impacts on SKR foraging that we detected. Future research is needed to understand the relationship between spectrum and light intensity on nocturnal rodent foraging decisions, especially given the rapid technological advancement in economical LED technology that allows for a range of spectral signatures (Longcore et al., 2018).

It is well known that, for prey species, when seeking and processing food, the forager balances energetic gain with safety from predators (Brown and Kotler, 2004; Lima and Dill, 1990). In response to perceived predation risk, animals employ a range of behavioral tactics including modifications to habitat and space use,

vigilance, and foraging behavior (Creel et al., 2007). These behavioral modifications carry substantial costs that can manifest through impacts on health and fitness (e.g. reduced energy income, growth, body condition, survival, or reproductive success), and have population-level and even ecosystem-level consequences (Creel et al., 2007; McHuron et al., 2018; Pirotta et al., 2018; Preisser et al., 2005). Ecosystem-level impacts are evident through alterations to trophic cascades (Preisser et al., 2005) or competitive interspecific interactions (Francis et al., 2012; Gerrish et al., 2009). Taken together these multilevel impacts may alter conservation outcomes for at-risk species. Our results indicate that anthropogenic disturbance, in the form of ALAN, negatively impacts SKR energetics through the alteration of foraging decisions. Future research is needed to evaluate the impacts of ALAN on fitness and persistence over the long-term. Given that populations of at-risk species, such as SKR, are already small or declining and many are isolated, the additional threats from human activities such as ALAN have the potential to drive these species to extinction. One of the main drivers of species declines is the loss, fragmentation, conversion and degradation of habitat (Groom et al., 2014). ALAN may exacerbate the direct effects of habitat loss by degrading the quality of the remaining habitat.

5. Conclusions

Artificial lighting is one of the fastest growing environmental pollutants, with the potential for devastating long-term ecosystem level consequences (Longcore and Rich, 2004; Navara and Nelson, 2007). For SKR, ALAN alters foraging decisions. As natural areas become more impacted by anthropogenic light this could contribute to an interaction with other disturbances, such as acoustic noise. The cumulative effects of urbanization may lead to the extirpation of endangered or threatened species. As an endangered species, it is important that remaining SKR habitats are not indiscriminately exposed to artificial light. We recommend that SKR land managers minimize artificial light near SKR habitat, orienting lights away from SKR habitat, shielding lighting to reduce light dispersion, or using motion sensor lighting or an on/off switch to allow for periods of darkness when human use is not required. Core SKR habitat should be separated from the light by a buffer of unlit native vegetation of a minimum of 50 m. If a temporary lighting disturbance is necessary it should be scheduled to coincide with the full moon to concentrate impacts during nights when kangaroo rat activity is lowest. Methodologies like these could reduce the negative impact of ALAN on SKR. Finally, more studies of ALAN on SKR population level impacts such as rates of survival and reproduction are needed.

More broadly, the effect of ALAN on small rodent energetics may be particularly problematic in the context of global climate change. A behavioral shift under ALAN, combined with food stressed conditions due to forecasted weather patterns, might not allow these species to persist in areas exposed to ALAN. Future studies should assess the consequences of ALAN avoidance by small rodents within the context of the greater community level response. The behavioral modification of small rodents that are often primary seed dispersers of native plants and ultimately the potential removal of these keystone species may lead to complex and far reaching indirect effects on the communities in which they live.

Declaration of competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.114566.

Author statement

D.M.S. conceived of the research, developed the study design, analyzed and interpreted the data and acquired permissions and funding to support the project. A.K.B., T.B.W. and D.M.S. performed the experiment, T.B.W. and D.M.S. curated the data, produced the figures and wrote the first draft of the paper. A.K.B. contributed in discussions and revisions.

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