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Bright lights, big city: an experimental assessment of short-term behavioral and performance effects of artificial light at night on *Anolis* lizards

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Abstract

With urbanization expanding into natural areas, it is increasingly important to understand how species subject to human-induced habitat alteration respond to novel opportunities and stressors. A pervasive consequence of urbanization is artificial light at night (ALAN), which previous studies have found introduces both costs and benefits for vertebrates. This understanding, however, primarily reflects findings from laboratory-controlled experiments or comparisons of wild populations in areas with long-standing differences in ALAN regimes. Here, we investigated the short-term costs and benefits for *Anolis* lizards during the period of initial exposure to ALAN using realistic light levels for urban areas (mean ± SD = 87.9 ± 36.7 lx at a distance of 3 m). As compared to controls, we hypothesized that adding ALAN would result in behavioral and physiological changes over the short term for brown anoles and their arthropod prey. In contrast to predictions, ALAN did not increase arthropod abundance or extend anole activity into the night. Structural habitat and sleep site use changed little in response to ALAN, which exposed about one-third of sleeping anoles in ALAN plots to light at night due to our manipulation. However, this direct light exposure resulted in lizards being more easily roused from sleep compared to lizards sleeping in the dark in control plots or in shadows in ALAN plots. The apparent inability of some anoles to adjust their sleep sites to avoid ALAN exposure may have contributed to their increased responsiveness at night and decreased locomotor endurance in the day. Our study suggests brown anoles can experience higher short-term costs than benefits during initial exposure to ALAN.

Keywords Anole · Artificial light · Behavior · Habitat use · Performance · Urbanization

Introduction

Cities are microcosms of global environmental change. Organisms in cities experience a litany of global change phenomena including human-induced climate change (i.e., urban heat islands), habitat transformation and species invasions (Rizwan et al. 2008; Forman 2014). One aspect of global change strongly tied to urbanization is artificial light at night (ALAN; Kyba et al. 2017). Human use of ALAN over the last century has altered natural cycles of light to varying degrees (Gaston et al. 2014), resulting in a diverse array of responses to ALAN for organisms (e.g., foraging activity, physiology and reproduction) and communities (e.g., predator-prey interactions, species diversity and abundance) (Rich and Longcore 2006; Navara and Nelson 2007; Gaston et al. 2015; Ouyang et al. 2018). Despite our increasing knowledge of organismal responses to ALAN and their potential costs and benefits, we still lack an understanding of how quickly organisms respond to novel ALAN, when costs and benefits emerge, and how these change over time.

The costs and benefits of ALAN for organisms may vary over time as a result of behavior, developmental plasticity and evolution as well as their direct and indirect interactions with other species in the community affected by ALAN (e.g., Knop et al. 2017). Among the potential costs of ALAN are disrupted circadian rhythms (e.g., Dominoni 2015; de Jong et al. 2016); suppressed melatonin, which can decrease immune and anti-

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oxidant function (e.g., Durrant et al. 2015); increased risk of predation (Silva et al. 2017); and decreased or less effective sleep (e.g., Moore et al. 2012; Ouyang et al. 2017), which may have carry-over effects on daytime behavior (Kurvers et al. 2018). On the other hand, organisms may also benefit from ALAN through increased foraging opportunities (termed the "night-light niche"; Garber 1978) due to increased feeding times and increased abundance or concentration of prey attracted to lights, both in the night and day (e.g., Rydell 1992; Petren et al. 1993; Davies et al. 2012; Welbers et al. 2017). Moreover, ALAN may alter the perception of daylength (Dominoni and Partecke 2015; Russ et al. 2015), which is a key stimulus for reproductive activity in many species. This can result in an earlier or longer reproductive period that could enhance fitness (e.g., Robert et al. 2015; Thawley and Kolbe 2020; but see Both et al. 2006).

The costs and benefits of ALAN may be complex and dependent on the species and ecological context. Most previous research on the effects of ALAN comes from two main types of studies. First, studies of relatively short-term, experimental exposure under laboratory conditions have often focused on ALAN's impacts on circadian rhythms, hormonal regulation and reproduction (e.g., Bedrosian et al. 2011). These studies have revealed substantial and diverse physiological effects from even low levels of ALAN (e.g., ~5–12 lx used by Borniger et al. 2014; Fonken and Nelson 2013). Second, field-based comparative studies of long-established night-lighting regimes (i.e., years to decades) are useful for assessing the consequences of long-term exposure for reproduction (e.g., Miller 2006; Robert et al. 2015) and community composition (e.g., Davies et al. 2012; Knop et al. 2017). Despite a wealth of knowledge gained using these two approaches, they have focused primarily on mammals and birds, with a lack of research on reptiles (Gaston et al. 2015; Russart and Nelson 2018). Moreover, studies of wild populations are lacking (Gaston et al. 2015), with few studies that experimentally manipulate light in the field to assess the initial effects of ALAN and its immediate consequences for behavior, performance and ecological interactions (but see Sanders et al. 2018). Such studies are essential for understanding effects of ALAN on organisms outside the laboratory and before communities respond to long-term exposure (Petren et al. 1993; Ouyang et al. 2017; Ouyang et al. 2018). Therefore, linking rapid introduction of ALAN to fitness in nature will require field studies that experimentally expose previously naïve populations to ALAN while leaving unmanipulated controls for comparison (Lapiedra 2018). This experimental design can capture the initial performance and behavior changes associated with exposure to ALAN, which are lost in most field studies, and allow researchers to contrast the costs and benefits of adopting the "night-light niche."

Anolis lizards (or anoles) are an excellent model system for conducting field-based experiments to assess the effects of ALAN. First, many *Anolis* species occupy urban areas (e.g., Kolbe et al. 2016), and although there are no known nocturnal anoles, numerous species are active and forage at night near artificial lights (Meshaka et al. 2004; Brown and Arrivillaga 2017; Maurer et al. 2019). In fact, Garber (1978) originally described the "night-light niche" based on observations of the crested anole (*Anolis cristatellus*) foraging at night under lights in Puerto Rico. Moreover, anoles foraging under lights at night do so under the risk of predation (Perry and Lazell 2000). Second, past research shows that anoles exhibit sleep-site selection, sleeping on perches that are higher, narrower and more horizontal as well as more often on leaves compared to perches used during the day (Singhal et al. 2007). Compared to daytime perches, these sleep sites are thought to allow better detection of approaching organisms in the arboreal environment, making anoles less vulnerable to predation (Hamilton 1982; Lima et al. 2005). We also know that light pulses during the nighttime dark period induce locomotor activity in laboratory studies of *Anolis* species (Moore et al. 2012), suggesting the potential for ALAN to disturb sleep quality or duration under field conditions. If ALAN disturbs sleep or increases the susceptibility of anoles to predation, then they may respond by shifting their sleep sites to avoid exposure to light at night. Third, anoles are amenable to observation and experimental manipulation in the field. Most species have relatively small home ranges, and lizards can be easily observed both during the day and night. Furthermore, anoles have a long history of behavioral and ecological studies under natural (non-ALAN) conditions (reviewed in Losos 2009), which informs predictions and provides ecological and evolutionary context for any behavioral or performance responses as a result of ALAN. For example, numerous studies have evaluated the structural habitat use of anoles in different habitats and when co-existing with different competitors and predators, both during the day and night (reviewed in Losos 2009; Singhal et al. 2007; Lapiedra et al. 2017).

The overarching goal of this study was to examine the short-term costs and benefits of ALAN during the period of initial exposure to this dramatic environmental change. We experimentally manipulated exposure of free-living brown anoles (*Anolis sagrei*) to ALAN by illuminating small plots at an unlit location using halogen bulbs commonly used as landscape lighting in the surrounding urban area. Lighting in nearby control plots was left unchanged. We focused on assessing changes in behavior and performance because they are among the most relevant potential consequences of ALAN over the short-term based on lab studies and field observations (de Jong et al. 2015; Kurvers et al. 2018; Russart and Nelson 2018). We predicted that diurnal brown anoles would benefit from ALAN through increased foraging opportunities in the form of extended foraging during the night (Russ et al. 2014), and increased abundance of arthropod prey attracted to the lights, which could be a benefit during both night and day (Davies et al. 2012). In terms of costs, we predicted lizards in plots exposed to ALAN would show decreased daytime endurance as well as rates of display, movement, foraging and social interaction due to nighttime activity or sleep disruption. We also predicted that lizards in ALAN plots would respond faster to nighttime disturbance due to decreased sleep quality or increased vigilance (Moore et al. 2012; Yorzinski et al. 2015). This would be detrimental if lizards waste energy when predation risk is low; however, it could also be beneficial if it results in enhanced anti-predator response under the threat of predation. Lizard perch use during the day and sleep-site use at night may also respond to ALAN exposure, but whether potential responses are positive or negative depends on many factors, such as predation risk.

Methods

Study site and experimental design

We conducted this experiment at the Montgomery Botanical Center in Coral Gables, Florida (29°39′40” N, 80°16′57.5” W) from June 20–August 14, 2013. We identified an approximately 175 m × 75 m study area consisting of mulched beds planted with cycads and a mix of native and non-native trees as well as interstitial grassy areas (Figs. S1 & S2). The entire area was not previously exposed to direct artificial lighting and experienced only sky glow and natural fluctuations in lunar illumination at night (0.0–0.1 lx as measured in study plots prior to ALAN exposure; Thawley and Kolbe 2020). This part of the Miami metropolitan area experiences artificial sky glow 10–20 times greater than natural sky brightness (Falchi et al. 2016). Using the existing cycad beds (Fig. S2), we established 20 plots (Fig. S1; mean ± SD = 86 ± 32 m^2; range = 41–149 m^2) from which we collected data on diurnal and nocturnal lizard habitat use, behavior and performance as well as arthropod abundance. After four weeks of pre-treatment data collection (June 20–July 18, 2013), we used one 150-watt halogen floodlight (GE, size PAR 38) to illuminate a large portion of the ground and vegetation within each of 10 randomly selected plots during the night (ALAN treatment plots) starting on July 18, 2013, while 10 plots remained unaltered controls (Fig. S2). We positioned floodlights on the ground pointing toward vegetation to replicate typical lighting conditions used in landscaping and home security, and to minimize illuminating other plots. Treatment plot lights turned on 30 min before sunset and turned off 30 min after sunrise. We measured light intensities at a distance of 3 m directly in front of the floodlights in the 10 ALAN plots using a TES 1332A Digital Lux Meter, and in a single plot, we measured light intensities at 1-m intervals from 1 to 9 m directly in front of the floodlight. Although our chosen halogen bulb emits predominantly yellow and red spectra (Fig. S3), which are not strong attractants for insects (Justice and Justice 2016), we aimed to replicate typical conditions that arthropods and anoles would experience in the local urban area. We continued to collect data on lizards and arthropods for almost four weeks after the onset of the ALAN treatment from July 20–August 14, 2013. Although five *Anolis* species were present at this site (i.e., *A. carolinensis, A. cristatellus, A. distichus, A. equestris,* and *A. sagrei.*), we focused on *A. sagrei* because this species represented 95% of all observations (Fig. S2). The brown anole (*A. sagrei*) is a small, diurnal lizard native to the northern Caribbean and introduced to Florida and many other parts of the world (Kolbe et al. 2004). Brown anoles occupy human-modified habitats where they are exposed to ALAN in both their native and non-native ranges (Schwartz and Henderson 1991; Meshaka et al. 2004).

Arthropod abundance

We sampled arthropods using two methods to assess whether abundance differed between ALAN-treatment and control plots and between the day and night as well as whether abundance changed over time. First, we used sticky traps to capture aerial and arboreal arthropods, coating both sides of standard sheets of transparency film (21.6 × 27.9 cm) with Tanglefoot adhesive and mounting the sheets on 1-m high posts. We counted all arthropods >2 mm in length as potential food items. Second, we created pitfall traps by burying bowls (500 ml) filled with water and a trace amount of detergent flush with the surface of the ground to capture terrestrial arthropods (Spiller et al. 2010). Each plot had a sticky trap and a bowl placed in roughly the center of the plot and approximately 0.5 m in front of the floodlight in ALAN plots. Sticky traps were wrapped in clear plastic, and arthropods from bowls were stored in 70% ethanol for later identification. Using these aerial and terrestrial methods, we sampled arthropods three times during the experiment: 1) on June 22, 2013, which was 26 days prior to initiating the ALAN treatment on July 18, 2013, 2) on July 26, 2013, which was eight days after beginning the ALAN treatment, and 3) on August 13, 2013, which was 27 days after starting the ALAN treatment and just prior to the end of the experiment on August 14, 2013. We collected different samples during the day and night by exchanging new aerial and terrestrial traps at dawn and dusk in each plot.

Brown anole behavior - structural habitat use, sleep site use, displays, movements and interactions

In all plots during both pre- and post-ALAN periods and during the day and night, we assessed structural habitat use of lizards. Habitat use observations at night are the same as sleep site use (Singhal et al. 2007). We measured several aspects of perch use by lizards including height (cm), diameter (cm), inclination (degrees) as well as lizard orientation (degrees) on its perch and exposure to artificial light in treatment plots during the night (i.e., light or dark). For each lizard, we recorded age class (i.e., adult, juvenile, or hatchling) and sex (i.e., male or female) for adult lizards. We sampled plots no more than once per day or night to avoid collecting multiple observations of the same lizards on a given day. However, repeated measures of the same lizards may have occurred over the course of the study.

We also conducted 20-min focal observations of adult lizards during the day and, if active, during the night. A total of at least one hour of observations was conducted for both males and females in each plot for both the pre- and post-ALAN time periods. For each undisturbed adult brown anole, we recorded the number of displays (i.e., push-ups, headbobs and dewlap extensions), movements (i.e., crawling, running, jumping and perch changes), and interactions (i.e., social with conspecifics, congeners, mating and foraging). Data were analyzed as the total number of events recorded using models that included observation time as a covariate. We did not collect enough data on interactions to analyze these behaviors, so we excluded this category from further analyses.

Brown anole performance - escape response at night and endurance during the day

To evaluate the effect of artificial lighting on lizards at night, we approached sleeping lizards and, after ensuring that our presence had not disturbed them, we simulated predator approach by tapping on their sleeping perch. We quantified escape response as the number of times we needed to tap the vegetation on which they were sleeping before they initiated escape (i.e., moving at least one body length). We first assessed escape responses to compare anoles in control and ALAN plots regardless of whether or not individual lizards in the ALAN plots were sleeping on perches directly exposed to light at night. We then assessed a separate group of lizards in only the ALAN plots, recording whether the sleeping anole was exposed to light at night or in the dark (typically in the shadow of a leaf).

To assess whether artificial lighting at night had a carryover effect on lizards during the day, we measured endurance of adult lizards from control and ALAN plots. We captured adults of both sexes, recorded their body temperature using a thermocouple (K-type, 36-gauge, 0.13 mm diameter) and digital thermometer (Omega HH802U), and immediately transferred them to a 109 × 46 × 54 cm plastic arena set up in the shade in the field. Endurance trials consisted of chasing lizards around the arena by hand at a steady pace until they could no longer right themselves for at least 15 s when flipped onto their backs (Kolbe et al. 2014). We measured endurance as the total time of activity before a lizard reached this point. We measured body temperature again at the conclusion of each trial along with body mass, which was used as a covariate in the analysis. Lizards were only sampled from plots that had not been disturbed during the previous night.

Statistical analyses

We tested for mean differences in arthropod abundance as sampled in our traps using mixed models in R using the function "lme" in the R package "nlme" (Pinheiro et al. 2020). We separated models by both sampling method (i.e., bowls and sticky traps) and by day and night samples, given that many arthropods have taxon-specific patterns of activity. In all cases, statistical models included fixed factors for experimental treatment (i.e., ALAN vs. control) and time period (i.e., three time periods with the first being pre-ALAN exposure) as well as the interaction between experimental treatment and time period. We included plot as a random effect in these statistical models. For analyses of bowls, numbers of arthropods captured were log-transformed to follow normal distributions. We analyzed the total number of arthropods captured as well as numbers in each of the three most common orders: Diptera, Hymenoptera and Crustacea. Sample sizes for Araneae and Coleoptera were too small to analyze separately. For analyses of data from sticky traps, models followed a Poisson distribution, so we used mixed models using the function "glmer" in the R package "lme4" (Bates et al. 2015).

To evaluate whether our ALAN treatment altered the habitat use of anoles, we used mixed models using the function "lme" in R (Pinheiro et al. 2020). Models analyzing changes in perch height, perch diameter, perch inclination and lizard orientation included sex/size categories (i.e., adult male, adult female, juvenile, hatchling), and the interaction between experimental treatment and time period. The models also included plot as a random effect and followed normal distributions. Given known differences between habitat use during the day and night (i.e., sleep site use) in anoles (e.g., Singhal et al. 2007), we analyzed data for the day and night separately.

Pre-ALAN exposure to light at night was inferred to be absent given the lack of artificial lighting in our study plots and lack of lizards exposed to light at night in control plots after the initiation of the ALAN treatment. We therefore quantified light at night exposure after the ALAN treatment was initiated but did not conduct statistical analyses of these data.

Behavioral measurements followed an over-dispersed Poisson distribution and thus were modelled following a quasi-Poisson distribution using the "glm" function in base R (R Core Team 2015). For display and movement behaviors, models included the interaction between experimental treatment and time period. For these behavioral traits, models included observation time as a covariate. Sexes were analyzed in separate models. Plot could not be included as a random effect due to sample size limitations (i.e., not enough individuals were sampled within each plot by each sex/size category).

We tested for a difference in the number of taps needed to initiate an escape response at night using non-parametric Wilcoxon tests in JMP version 9 (JMP 2010). We conducted two analyses on separate groups of lizards, comparing anoles in ALAN and control plots as well as lizards exposed to light or in the dark within ALAN plots. We evaluated differences in endurance of lizards from our ALAN treatment and control plots using analysis of covariance (ANCOVA) with lizard mass as a covariate in JMP version 9 (JMP 2010). We also determined whether endurance was related to lizard body temperature at the start or end of trials using linear regression in JMP version 9 (JMP 2010). Plot was not included as a random effect due to sample size limitations.

Results

Light intensities at 3 m in front of the floodlights in the 10 ALAN plots ranged from 23.4 to 156.5 lx (mean ± SD = 87.9 ± 36.7). During the afternoon, light intensities at the same locations within the plots ranged from 365 to 1070 lx (mean ± SD = 956 ± 165). In ALAN treatment Plot 13, light intensity decreased from a maximum of 468.0 lx at 1 m from the floodlight to 6.0 lx at a distance of 9 m (Table 1).

Arthropod abundance

The most common arthropod orders sampled in bowl traps were Crustacea, Diptera and Hymenoptera (Table 2). Contrary to our predictions, the experimental ALAN treatment did not increase the number of arthropods during the day or night when sampled by either method (Tables S1 & S2). ALAN treatment did not increase the total amount of arthropods captured during the day using bowl traps (Table S1; experimental treatment x time period interaction: $t = -0.57$, $df = 39$, $p = 0.57$). The same was true for samples collected during the night (Table S1; $t = 0.32$, $df = 36$, $p = 0.75$). The abundance of arthropods captured tended to decrease over time during the day (Table S1; $t = -1.79$, $df = 39$, $p = 0.08$), a tendency that was significant for samples collected during the night ($t = -4.27$, $df = 36$, $p < 0.001$).

When analyzing arthropod abundance separately by order, the interaction between experimental treatment and time period was never significant (Table S1; all $p > 0.20$). We did not find a general effect of experimental treatment for any of the groups analyzed (Table S1; all $p > 0.35$). At night, the overall decrease in the number of arthropods captured over time remained significant in separate analyses of Crustacea, Diptera and Hymenoptera (Table S1; all $p < 0.02$). For samples collected during the day, this decrease over time was only significant in the case of crustaceans (Table S1; $t = -3.01$, $df = 39$, $p < 0.01$).

Table 2 Numbers of arthropods sampled in bowl traps during the day and night as well as combined. Numbers for the five most common arthropod Orders are shown separately

Taxon	Day	Night	Combined
Araneae	22	35	57
Coleoptera	13	27	40
Crustacea	1022	856	1878
Diptera	1364	720	2084
Hymenoptera	1172	1604	2776
Others	24	74	98
Total	3617	3316	6933

We sampled an order of magnitude fewer arthropods in sticky traps ($N = 210$) compared to bowl traps ($N = 6933$; Table 2). When analyzing sticky trap samples collected during the day and night separately, we found no effect of experimental treatment, time period or their interaction on the number of arthropods captured (Table S2).

Brown anole behavior

We observed habitat use for a similar number of lizards during the day ($N = 2460$) and while sleeping at night ($N = 2257$) across the two months of the study. As lizards were not individually marked, this may include multiple observations of the same individuals over the experimental period. Lizards used both natural (e.g., cycads, palms, trees) and artificial (e.g., PVC, rebar, plastic plant signs) substrates in plots (Table S3). The initiation of the experimental ALAN treatment had some effects on structural habitat use (Table S4); after exposure to ALAN, lizard orientation was more horizontal during the day (lizard orientation: $t = 2.04$, $df = 2016$, $p = 0.04$) and they used more horizontal perches during the night (perch inclination: $t = -2.29$, $df = 2009$, $p = 0.02$). The interaction term between experimental treatment and time period was not significant in models for other aspects of habitat use

Table 1 Light intensity produced at 1-m intervals by halogen floodlights used in our ALAN treatment plots. Data are from Plot 13

Distance from floodlight (m)	1	2	3	4	5	6	7	8	9
Light intensity (lux)	468.0	156.0	76.4	39.0	27.2	17.6	11.2	7.4	6.0

during the day (perch height: $t = 0.03$, $df = 2104$, $p = 0.98$; perch diameter: $t = 1.71$, $df = 1607$, $p = 0.08$; perch inclination: $t = -0.31$, $df = 2104$, $p = 0.76$) or sleep site use at night (perch height: $t = -1.44$, $df = 2035$, $p = 0.15$; perch diameter: $t = 0.54$, $df = 2018$, $p = 0.59$; lizard orientation: $t = -1.54$, $df = 1849$, $p = 0.13$).

Our experimental treatment resulted in exposure to light at night for approximately one-third of lizards in ALAN plots depending on the sex/size class compared to no lizards being exposed to light at night in post-treatment control plots (Table S5). This provides good evidence of the efficacy of our experimental manipulation.

We conducted focal behavioral observations for a similar total number of adult male ($N = 148$) and female ($N = 142$) brown anoles in ALAN treatment and control plots before and after exposure to light at night. We only observed three brown anoles active at night, two females and one male moving for short periods of time in ALAN plots after the initiation of light at night. No foraging at night was observed. This small number of observations of activity was therefore too small for analyses of behavior at night. Similar to habitat use during the day, the ALAN experimental treatment was not associated with any behavioral differences in displays or movements for adult males or females (Table S6).

Brown anole performance

Tapping perches elicited escape responses from lizards ranging from short movements along a perch to jumping off of their sleeping perch entirely. When comparing escape responses of brown anoles at night we found a 78% reduction in the number of taps needed to arouse lizards from sleep in ALAN treatment plots compared to control plots (Fig. 1a; Wilcoxon: $Z = 7.4$, $p < 0.0001$, $N = 112$). To further investigate whether this difference in escape behavior was due to direct exposure to artificial light, we compared the arousal from sleep for brown anoles sleeping in light versus dark patches within ALAN treatment plots. We found an 84% reduction in the number of taps needed to disturb lizards when they were sleeping in the light compared to the dark (Fig. 1b; Wilcoxon: $Z = 4.1$, $p < 0.0001$, $N = 62$).

To assess whether ALAN exposure had carryover effects into the day, we measured the endurance of lizards from 10 plots evenly distributed between ALAN treatments and controls. Endurance during the day was 28% lower for lizards from ALAN treatment plots compared to controls (Fig. 2; ANCOVA: Treatment: $F_{1,60} = 28.5$, $p < 0.0001$; mass covariate: $F_{1,60} = 18.8$, $p < 0.0001$; $R^2 = 0.45$; $N = 63$). There was no relationship between endurance and lizard body temperature at the start ($p = 0.24$) or end ($p = 0.94$) of trials.

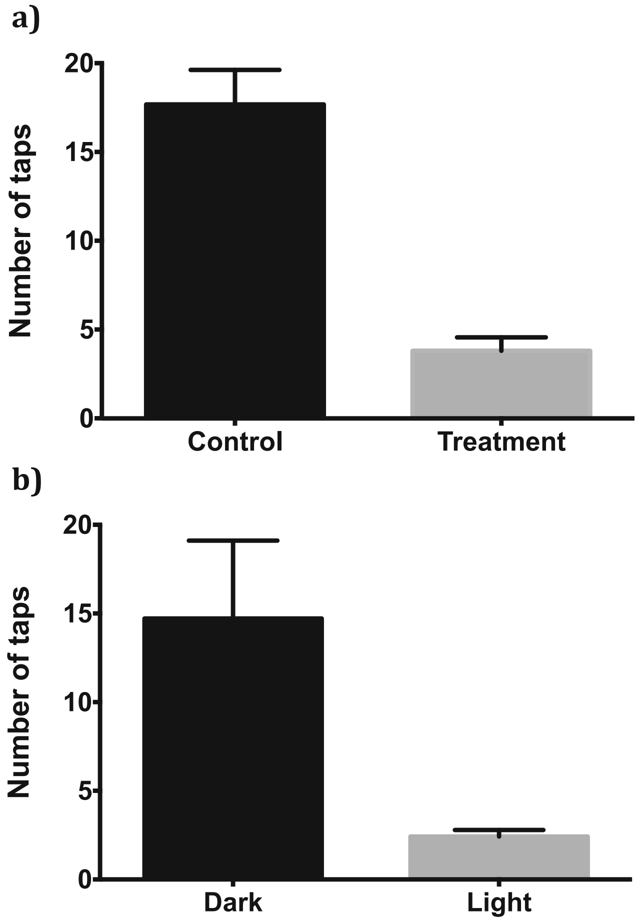

Fig. 1 Mean (± SE) for the number of taps needed to elicit an escape response (i.e., moving at least one body length) from sleeping brown anoles perched on vegetation comparing a) lizards from control ($N = 50$) and ALAN treatment ($N = 62$) plots and b) lizards from ALAN treatment plots at sleeping sites in the dark (not exposed to ALAN; $N = 7$) and in the light (directly exposed to ALAN; $N = 55$). The discrepancy in sample size for lizards in the dark and light was due to the majority of lizards being exposed to light in ALAN plots. On average, lizards in ALAN plots showed a 78% reduction in the disturbance needed to produce an escape response, and within ALAN plots, lizards exposed to direct ALAN showed an 84% reduction

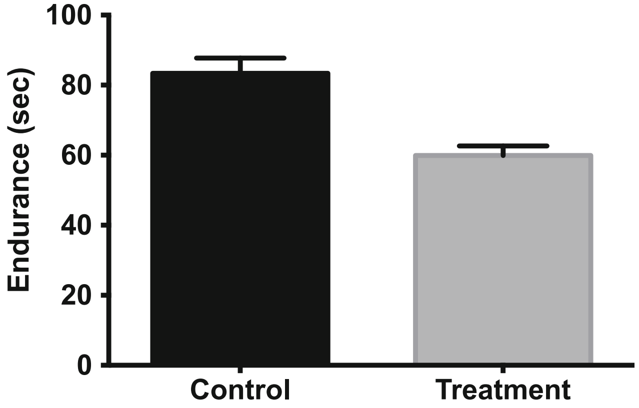

Fig. 2 Mean (± SE) seconds of endurance for brown anoles from control ($N = 30$) and ALAN treatment ($N = 33$) plots. On average, ALAN results in a 28% reduction in daytime endurance for lizards

Discussion

Our field-based experiment was designed to assess whether brown anoles exhibit behavioral and performance changes during the initial weeks of exposure to novel ALAN conditions, allowing us to evaluate potential costs and benefits. In contrast to predictions, ALAN did not increase arthropod abundance at our site or extend the activity of lizards into the night. Therefore, lizards in treatment plots did not appear to experience the predicted benefits of ALAN related to foraging (i.e., increased abundance and access to arthropod prey). Support for predicted costs of ALAN in our study population were mixed. Brown anole behavior (i.e., displays and movement) during the day did not change after exposure to ALAN. Additionally, we did not detect any shifts in structural habitat use during the day or sleep-site use at night, which resulted in about one-third of sleeping brown anoles in ALAN plots being exposed to light at night due to our experimental manipulation. This direct exposure to light resulted in lizards being more easily aroused from sleep compared to sleeping lizards in the dark or in the shadows. The apparent inability of some brown anoles to adjust their sleep sites to avoid exposure to ALAN may have contributed to their increased responsiveness at night and decreased locomotor endurance in the day.

We predicted brown anoles in ALAN plots would benefit from increased prey abundance and extended foraging opportunities. Previous research shows that ALAN attracts insects (Petren and Case 1996; Eisenbeis 2006; Owens and Lewis 2018) and increases local abundance of many invertebrate groups (Davies et al. 2012). These represent potential prey for anoles, which are known to forage at night under artificial lighting (Garber 1978; Perry and Lazell 2000; Meshaka et al. 2004; Perry and Fisher 2006). Thus, access to greater prey resources should encourage foraging at night. However, our ALAN treatment did not increase arthropod abundance in the day or night based on our trapping methods. Thus, our experimental manipulation found no evidence for a primary potential benefit of ALAN in the short term, that is, an increase in potential prey. Our choice of halogen bulbs reflects realistic lighting used in urban areas for landscaping and home security; however, they have low emittance in the color spectrum shown to most strongly attract insects (e.g., Justice and Justice 2016; Fig. S3). Thus, it is important to keep in mind that the color spectrum and brightness of our halogen bulbs likely contributed to the lack of insects. Pesticide use at the botanical garden and in the surrounding neighborhoods that generally reduced arthropod abundance or phenological and weather-related fluctuations in arthropods would be unlikely to affect our ALAN and control treatments differently. It is possible that lizards or other insectivores disproportionally reduced prey resources in ALAN plots masking ALAN-induced increases. However, as brown anole foraging activity during the day did not differ between ALAN treatment and control plots, this seems unlikely.

Anoles are almost exclusively visual predators and are likely unable to forage in naturally dark conditions (Fite and Lister 1981). As such, even in the absence of increased arthropod abundance, anoles could still benefit from ALAN, as it should support foraging during night when it would otherwise be impossible. However, we observed only a few instances of brown anole activity at night, and lizards were never observed eating at night. It is possible that anoles did not engage in nocturnal foraging under ALAN because they lack the behavioral flexibility to take advantage of extended foraging on the time scale of our study. Given the frequency with which anoles are observed foraging under ALAN in other contexts, it is also possible that they may only forage under ALAN when experiencing the stimulus of supranormal arthropod abundance common at artificial lights, or when the benefit of increased food might outweigh potential costs of nocturnal foraging such as increased predation risk.

Organisms impacted by ALAN often increase activity, including foraging, both by extending activity in the evening and becoming active earlier in the morning (Dominoni 2015; Russ et al. 2015). We may have failed to detect some brown anole foraging at night if lizards increased activity pre-dawn instead of post-sunset when our surveys occurred (all night surveys ended before 2400 h). In Antigua, *Anolis leachii* showed similar levels of activity throughout the night, whereas *Anolis wattsi* showed an enormous spike in activity just before sunrise (Maurer et al. 2019). Thus, activity patterns at night may vary among species, and no data documenting nocturnal activity across the entire night exist for brown anoles. We found no support for one potential benefit of ALAN (i.e., increased foraging due to increased arthropods) over the short term for brown anoles at our site. Future research is needed to determine whether longer exposure to ALAN would result in increased arthropod abundance, as seen in other studies (Manfrin et al. 2017; Owens and Lewis 2018), and whether this results in foraging benefits.

We found no evidence that brown anoles altered the habitat they used for sleeping in response to our ALAN treatment. As a result, approximately one-third of sleeping lizards in our ALAN treatment were exposed to novel artificial light. It is difficult to know whether lizards adjusted their sleeping positions to avoid exposure to light at night. This would require marking individual lizards and identifying their sleep sites before and after initiation of the ALAN treatment, a feasible future study using anoles. We therefore cautiously interpret our findings as a lack of short-term behavioral flexibility in at least some individuals to avoid exposure to ALAN.

Anole sleep behavior is well characterized including a typical sleep posture and location, behavioral inactivity, increased stimulus threshold for arousal, and rapid reversibility to wakefulness (Lima et al. 2005; Singhal et al. 2007). Sleep is generally considered a vulnerable behavioral state, and many animals prefer to sleep in locations that are either less vulnerable to predation (e.g., denser vegetation) or that are more sensitive to predators approaching (e.g., flimsier perches) (Hamilton 1982; Lima et al. 2005). Anoles are known to sleep on higher and narrower perches (Singhal et al. 2007), which should be both less vulnerable and more sensitive to predators. Brown anoles in our study clearly followed this pattern of sleep-site use (Figs. S4 & S5); however, we did not observe an effect of the ALAN treatment on sleep-site use except for lizards sleeping in more horizontal positions. Anoles also sleep in more horizontal positions compared to their daytime habitat use (Singhal et al. 2007); however, the reasons why this position might be safer or afford more vigilance are unknown. Despite the expectation that lit perches would leave lizards more visible to potential predators, anoles did not appear to move to obviously safer sleeping locations away from ALAN exposure even when as close as a body length away. This may be because of a lack of behavioral flexibility in general, or at least over the several weeks of exposure to ALAN in this study.

If exposure to ALAN leads to an increase in perceived predation risk, we would predict a change to relatively vigilant (lighter) sleeping in response (Lima et al. 2005). The presence of both natural (e.g., moonlight) and artificial light at night can increase predation risk (Silva et al. 2017), and some organisms actively avoid nocturnally lit areas, presumably to reduce predation (Prugh and Golden 2014; Farnworth et al. 2018). Based on a previous lab experiment, we do know that light at night increases locomotor activity in a dose-dependent fashion for multiple species of anoles (Moore et al. 2012). Our results from tapping on the perches of sleeping lizards suggest direct exposure to light at night leads to quicker arousal of lizards (Fig. 1b). Yet, we cannot distinguish whether light directly reduces the ability of lizards to sleep or decreases their arousal threshold due to heightened perception of predation risk (i.e., an increase in vigilance). If the observed behavior ultimately increases effective anti-predator response, then this could be a conditional benefit under increased predation risk. Numerous potential nocturnal predators were observed at our study site, including feral cats, racoons, rats and snakes, but we did not quantify predator abundance. Although some costs to lighter sleep may occur simultaneously with anti-predator benefits, poor sleep with no change in predation risk would incur only costs, which might include increased metabolism or energy usage, disrupted endocrine function including increased levels of glucocorticoid (“stress”) hormones, compromised immune function, or decreased energy or performance in the future (Ouyang et al. 2017, 2018; Welbers et al. 2017).

One clear cost of ALAN observed in our study was decreased locomotor endurance for brown anoles from ALAN plots. Circadian disruptions, including altered sleep, can lead to altered melatonin levels, changes in patterns of reproductive and foraging activity, and metabolic disruptions (Dominoni 2015; de Jong et al. 2016). Lower quality and duration of sleep is associated with lower endurance and performance in humans (Belenky et al. 2003; Oliver et al. 2009). In *Anolis* lizards, laboratory studies of pineal glands using a flow-through culture system showed that light caused significant phase delays of the melatonin cycle, although species from brighter habitats were less sensitive (Moore and Menaker 2012). Brown anoles are typically found in partial to full sun habitats (Ruibal 1961; Losos 2009). Moreover, the spectral sensitivity for multiple *Anolis* species is similar to that of other terrestrial vertebrates with a peak near 550–560 nm (Fleishman et al. 1997), which corresponds to only moderate spectral output from the halogen bulbs used in our study.

Thus, brown anoles may be less sensitive to ALAN effects that could alter melatonin cycles and circadian rhythms (Moore and Menaker 2011, 2012). Alternatively, the average 28% reduction in endurance we observed could be due to changes in levels or diel cycles of corticosterone (CORT), which are disrupted by ALAN (Ouyang et al. 2018). As CORT helps regulate energy availability, including increases in energy during waking hours (Russ et al. 2015), disrupted cycles could negatively impact endurance. However, exposure to ALAN under lab conditions does not alter brown anole CORT levels, suggesting this mechanism is unlikely to cause observed reductions in endurance (Thawley and Kolbe 2020). Lower endurance could also be related to the quicker arousal observed for lizards exposed to light during the night. Indeed, anoles exposed to pulses of ALAN in the lab had increased levels of nocturnal locomotion in the absence of external stimuli including prey (Moore et al. 2012). Furthermore, if lizards move more but do not forage during the night, then their total available energy will decrease. If they are more vigilant or sleeping lighter at night, then one result could be having less energy to use during the day. Again, following marked individuals during the day and night could provide insight into our finding of lower endurance for lizards from ALAN plots. To oversimplify our findings, lizards sleep poorly and are tired in the next day.

Our results identify some short-term costs of ALAN, which contrast with perceived benefits from foraging based on observational studies of anoles after long-term exposure to ALAN (e.g., Garber 1978; Perry and Lazell 2000) and relatively short-term lab studies showing fitness benefits through increased growth and reproductive output of brown anoles (Thawley and Kolbe 2020). We found no evidence for short-term benefits related to prey abundance or extended foraging times. The lack of increased prey resources during our experiment might be the reason why we did not observe foraging activity at night. Light at night should have induced some locomotor activity at night as seen in the lab (Moore et al. 2012), and lizards exposed to light at night in our study did respond quicker to disturbance at night. Yet, the risk of foraging at night may outweigh the potential benefits of increased foraging if the odds of success are low (i.e., low prey abundance or constraints on active body temperatures). Future studies should independently manipulate insect abundance and ALAN to tease apart the effects of these factors on foraging activity at night. Brown anoles did not alter their behavior during the day or sleep-site use at night after exposure to ALAN. If animals do not exhibit behavioral responses that limit exposure to ALAN, then lab studies exposing organisms to ALAN may be ecologically relevant. However, our short-term field manipulation only lasted one month, so careful attention to exposure times is needed when comparing results from lab and field experiments. Longer term studies in both the field and lab may help illuminate outstanding questions in this system including over what time scales anoles change their behavior and whether variation exists in the ability of individual anoles to learn to exploit the night-light niche. One clear short-term cost detected in our study was decreased locomotor endurance during the day. Previous research in anoles shows that light at night suppresses melatonin in multiple *Anolis* species (Moore and Menaker 2011). However, the magnitude of melatonin suppression in anoles is relatively small compared to other vertebrates, and particularly reduced in brown anoles (Moore and Menaker 2011). To test for a mechanistic link between hormones and performance, lab-based experiments are needed that expose lizards to light at night, measure melatonin levels and assess locomotor and other types of performance.

In conclusion, our study revealed short-term effects of artificial light at night, even without the primary feeding response that we predicted would influence lizard behavior. Lizards exhibited altered behavior during nighttime surveys (i.e., heightened awareness) that carried over to dampened daytime performance (i.e., decreased endurance). Such changes in behavior and performance could have implications for anoles both as prey at night and predator during the day. These results suggest that animals encountering changes in nighttime lighting are subject to costs that are not always balanced by predicted benefits, particularly in animals without the flexibility to behaviorally adapt on short timescales. Ultimately it is the net ratio of costs and benefits that will determine the ability of populations to persist when encountering ALAN in cities. Finally, as ALAN increasingly illuminates our world at night, understanding the specific impacts of commonly used light sources in urban areas will allow us to more accurately predict species responses to realistic ALAN settings.

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Authors' contributions JJK and HAM conceived of this study and conducted the field work; all authors contributed to data analysis and interpretation; JJK wrote the first draft of the manuscript; all authors contributed to manuscript revisions and approved the final version of the manuscript.

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Data Availability Data are available from the authors upon request.

Compliance with ethical standards

Ethics approval The University of Rhode Island Institutional Animal Care and Use Committee approved protocols for use of live animals in this study (AN11–09-005).

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