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NOCTURNAL ACTIVITY OF ANTIGUAN LIZARDS UNDER ARTIFICIAL LIGHT

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***Abstract*.—Widespread human development has led to the proliferation of artificial light at night, an increasingly recognized but poorly understood component of anthropogenic global change. Animals specialized to diurnal activity are presented opportunities to use this night-light niche, but the ecological consequences are largely unknown. While published records make note of nocturnal activity in a diversity of diurnal taxa, few case studies have gone beyond isolated observations to quantify patterns of nocturnal activity, document animal behavior, and describe new species interactions. From 13 June to 15 July 2017, we conducted hourly nocturnal surveys to assess how two species of diurnal *Anolis* lizards (Leach's Anole, *Anolis leachii*, and Watt's Anole, *A. wattsi*) use artificial light on Long Island, Antigua. Our data show that both anole species foraged in artificially illuminated habitats and were more active prior to sunrise compared to the early night. Mark-resight data for a focal species, *A. leachii*, suggest that patterns of nocturnal activity were not significantly different between individuals. Finally, our behavioral observations for the two anoles and a third lizard species, the nocturnal Thick-tailed Gecko (*Thecadactylus rapicauda*), reveal a lack of agonistic interactions. Our study reveals an altered temporal niche for two diurnal Antiguan lizards and adds to a growing body of evidence documenting the broad influences of anthropogenic change on biodiversity.**

*Key Words.—*Anoles; *Anolis leachii*; *Anolis wattsi*; ALAN; artificial light at night; light pollution; night light niche

INTRODUCTION

As global anthropogenic change accelerates, the occurrence of artificial light at night is increasing in extent and density (Hölker et al. 2010; Gaston et al. 2015). Artificial lighting during dark hours alters natural light regimes under which animal behaviors have evolved. This ecological light pollution has important biological consequences, including changing animal activity patterns (Longcore and Rich 2004). Indeed, as a result of urbanization and artificial lighting, many diurnal species have been recorded extending or switching typical daytime behaviors into the night (e.g., Perry et al. 2008).

Plasticity in activity pattern can allow organisms to exploit the evolutionarily novel night-light niche (Garber 1978; Gaston et al. 2014), which may come with a variety of benefits and costs. For example, use of artificially lighted habitats can allow individuals to acquire additional energy by extending foraging times. Insectivores may forage on arthropods attracted to lights (Verheijen 1960), a behavior commonly observed in lizards (Perry and Fisher 2006; Martín et al. 2018). Activity at night may also allow for maintenance of territories, additional opportunities for courtship and reproduction, and avoidance of competition (Rich and Longcore 2006). Use of the night-light niche may also entail costs, including increased energy expenditure, non-optimal thermal conditions, disruption of endocrine function, increased competition, or increased susceptibility to some predators (Petren et al. 1993; Perry and Lazell 2000; Perry and Fisher 2006; Ouyang et al. 2018).

Despite a growing interest in the ecological effects of artificial light at night, its effects on animal behavior remain relatively underexplored. The availability of artificial light is especially relevant for animals whose dominant sense is sight, such as diurnal lizards of the genus *Anolis* (hereafter, anoles). Seventeen species of anole have been documented using artificial lights (Perry et al. 2008). Most anecdotal observations of nocturnally active anoles document foraging behaviors (Perry and Fisher 2006). Reports of displaying males (Robert Trivers, pers. comm.), courtship (Bowersox et al. 1994), and reproduction, however, suggest that a wider range of behaviors regularly occur around artificial

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lights (Wilson and Porras 1983). Yet, the diversity and prevalence of such behaviors used at artificial lights has not been systematically studied.

Other relevant questions about the use of the night-light niche remain unaddressed. For instance, detailed observations of activity patterns at artificial lights across the entire night have not been made in any anole species. Moreover, anecdotal reports that typify current literature do not follow specific individuals. Consequently, we lack basic information about whether individuals vary in their use of artificially lighted habitats. The demographics of individuals using lights at night are also unclear. While anoles of both sexes have been reported using lights at night, some observations (e.g., Powell and Henderson 1992) have suggested a bias towards young males. In sum, moving beyond an anecdotal listing of species using artificial lights is needed. Determining the behaviors, demographics, and individual variation associated with use of artificial lights at night is necessary for understanding the ecological and evolutionary impacts for diurnal organisms.

In summer 2017, we documented the nocturnal behavior and activity patterns of two species of diurnal anole, Leach's Anole (*Anolis leachii*) and Watts' Anole (*A. wattsi*), at an artificial light source in Antigua, West Indies. During normal diurnal activity, these species occur alongside various other lizards, most notably Griswold's Ameiva, *Ameiva griswoldi* (Kolbe et al. 2008), and occupy the same habitats used by nocturnal geckos (e.g., native Thick-tailed Geckos, *Thecadactylus rapicauda*, and non-native tropical House Geckos, *Hemidactylus mabouia*). We assessed the types and timing of anole behaviors shown through the night and monitored marked individuals to assess whether individuals consistently used the novel niche and how this behavior varied between individual anoles.

MATERIALS AND METHODS

From 13 June to 15 July 2017, we performed nightly lizard surveys on Long Island, Antigua (17.156235°N, 61.751053°W) from approximately 2000 to 0600. Over this period, sunset ranged from 1841 to 1844 and sunrise from 0533 to 0541. We surveyed an approximately 28 m^2 porch featuring a single artificial light source that pointed straight down from the ceiling (height: 3 m). We conducted visual surveys every hour per night except during occasional periods in the middle of the night (e.g., 2200–0100) when we were only able to survey opportunistically. For every individual lizard observed, we recorded the time, perch location, and height. At the start of the study, and when new individuals appeared thereafter, we captured and marked each *A. leachii*. For each individual, we determined its sex, measured its snout-vent length (SVL), and gave each a unique alphanumeric dorsolateral mark allowing for future identification.

To assess whether individual *A. leachii* varied in their use of the night-light niche, we calculated the mean proportional similarity (mean PSi; an index of inter-individual variation, also known as individual specialization) between individual and cumulative (population) distributions of activity (following methods in Kamath and Losos 2017). This procedure tests whether patterns of nocturnal activity observed in each individual diverged from those observed for the entire population. We calculated individual and population level indices of individual specialization (PSi) using the PSicalc function in the RInSp R package (Zaccarelli et al. 2013). The *P* value was calculated by comparing observed distributions to randomly sampled distributions from the population distribution. Values of PSi range from one (low inter-individual variation) to zero (high inter-individual variation). We performed all analyses in R v. 3.2.2 (R Core Team 2015) using RStudio (version 1.0.136, R Team 2015) with $\alpha = 0.05$.

RESULTS

We made 99 observations of *A. leachii*, *A. wattsi*, and *T. rapicauda*. No other lizard species were observed. We frequently detected all three species during the same survey, and on several occasions detected multiple *A. leachii* individuals on the same survey. We did not observe any intra- or interspecific agonistic interactions or visual displays (e.g., headbobbing, push-ups, or dewlap extensions) during surveys.

The three lizard species exhibited distinct perch heights: *A. leachii* typically perched high on walls, between 2.4 and 3.0 m, *A. wattsi* was only observed on the porch floor, and *T. rapicauda* displayed a variable perch height, ranging from behind shutters at approximately 1.2 m to using the ceiling at 3.0 m. We observed the lizards feeding on a variety of nocturnal invertebrates, particularly small insects and Lepidoptera; foraging appeared to be the primary behavioral mode. We also made isolated observations of *A. leachii* catching and eating arthropods including a cockroach (Blattodea) and a tarantula (*Cyrtopholis* sp., likely *C. bartholomaei*; Fig. 1).

Our mark-resighting approach resulted in 78 *A. leachii* detections with eight confirmed individuals (five sightings were attributed to unmarked individuals), 12 *A. wattsi* sightings of one confirmed individual, and nine sightings of *T. rapicauda* (individuals not marked). We were able to definitively determine the sex of six *A. leachii* males based on scales at the base of the tail by the cloaca, and we expect that the remaining two *A. leachii* individuals were also male based on size and behavior. *Anolis wattsi* is sexually dimorphic in color (Lynn 1957), and the single individual we observed was male.

Figure 1. An adult male Leach's Anole (*Anolis leachii*) forages on a tarantula (*Cyrtopholis* sp.) under an artificial light source on Long Island, Antigua, in summer 2016. (Photographed by Alexandra L. Fireman).

Our surveys starting roughly one hour after sunset revealed activity patterns for *A. leachii* and *A. wattsi* that were both right-shifted (relative to midnight as the center of the x-axis; Fig. 2). The detections for *A. wattsi*, however, were densely distributed around 0500 resulting in a pronounced unimodal peak, whereas *A. leachii* detections were more evenly distributed through the night (Fig. 2). There was no significant difference between individual nocturnal activity patterns for *A. leachii* (mean PSi = 0.41 ± [SD] 0.30, *P* = 0.732; Fig. 3). SVL measurements from four *A. leachii* individuals indicated a mean body size of 9.5 ± (SE) 0.13 cm; all of the individuals detected were of similar size.

Discussion

Our results illuminate several important aspects of the contemporary natural history of Antiguan lizards. First, we describe previously undocumented nocturnal behaviors in *A. wattsi* alongside the extensive use of a nocturnal light source by *A. leachii*. Second, our observations suggest the primary driver of nocturnal activity in anoles is foraging opportunity. Third, the observed nocturnal activity was skewed toward early morning hours. Fourth, use of the night-light niche was restricted to male anoles. Fifth, individual variation in *A. leachii* nocturnal activity appears to be limited, suggesting that all individuals are taking advantage of this novel resource in a similar way.

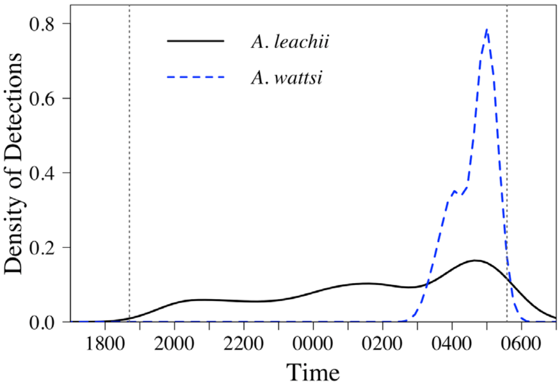

Figure 2. Overlapping density plots compare the temporal distributions of nocturnal detections for Leach's Anole, *Anolis leachii* (n = 78 observations), and Watts' Anole, *A. wattsi* (n = 12 observations). Sunset (1842) and sunrise (0535) are shown with dashed gray lines. Hourly surveys typically started at approximately 2000; the *A. leachii* curve extends earlier due to kernel density smoothing.

Our observations suggest that the primary driver of nocturnal activity in both species of Antiguan anole was the novel foraging opportunity presented by arthropods drawn to artificial lighting. We did not detect any behaviors associated with territorial maintenance or reproduction. Further, we did not observe intra- or interspecific agonistic interactions during our surveys (e.g., dewlapping). Because effective communication via the dewlap is specialized to specific photic conditions in anoles (Leal and Fleishman 2004), it is possible

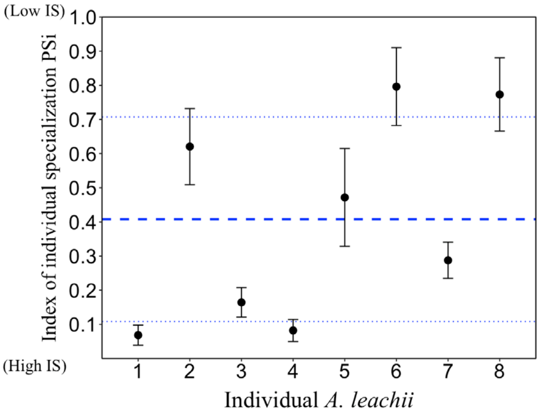

Figure 3. Indices of individual specialization (IS) in nocturnal activity for eight Leach's Anole (*Anolis leachii*) individuals (n = 78 observations). Points represent the mean pairwise similarity of that individual to all other individuals (PSi); error bars represent one estimated standard deviation. The mean population level of individual specialization is represented by a bold blue line and lighter dotted lines represent one standard deviation (mean PSi = 0.408 ± [SD] 0.30). Nightly surveys were conducted at an artificial light source on Long Island, Antigua, from 13 June to 15 July 2017, resulting in 73 detections of marked individuals.

that the evolutionarily novel photic conditions around artificial lights may disrupt normal communicative behaviors.

The use of the night-light niche by Antiguan anoles has interesting implications for interactions with coexisting nocturnal lizards. At our study location in Antigua, *T. rapicauda* were also present around the focal light source, with typically only a single individual observed. This species could represent an interspecific competitor for both *A. wattsi* and *A. leachii* or a potential prey source for large *A. leachii*; however, we did not observe any interactions between anoles and geckos, and nocturnally active *A. leachii* did not appear to be large enough to prey on observed *T. rapicauda* individuals. We also did not observe any other syntopic lizard species using artificial lights (e.g., *Ameiva griswoldi*). Future work should explore if use of the night-light niche confers physiological or demographic benefits (or costs) to anoles, potentially through competitive release, protection from predators, or subsidized predation on aggregated prey.

The observed nocturnal activity patterns for *A. leachii* and *A. wattsi* were right-skewed relative to a center of midnight, with 48% of observations occurring within 2 h prior to sunrise. Previous observations of anole nocturnal activity (including in *A. leachii*) were concentrated in the hours following sunset (e.g., Schwartz and Henderson 1991; Stroud and Giery 2013), though *A. carolinensis* activity has been documented roughly 2 h prior to sunrise (McCoid and Hensley 1993). With our observed activity concentrated closer to sunrise, this could provide evidence that the exploitation of the night-light niche by Antiguan anoles occurred because of an earlier start to diurnal activity, rather than an extension of diurnal activity past sunset. Because our first survey was typically 45–60 min after sunset, our inferences here are limited and we do not have data to rule out a post-sunrise activity period. Our anecdotal observations, however, support our finding of increased activity later in the night; we never observed *A. wattsi* during the hours around sunset, and several *A. leachii* exhibited behavior where they would appear for the first time in a survey night after midnight. Irrespective of specific nocturnal patterns, our daytime observations as well as those documented in previous studies in Antigua (e.g., Kolbe et al. 2008) suggest that activity remains much higher during the day than night for both species. Kolbe et al. (2008) present diel patterns in abundance that suggest a crepuscular schedule for *A. wattsi* and less pronounced peaks closer to midday for *A. leachii*. In sum, it is unclear if we will continue to see a gradual shift toward more nocturnal use of artificial lights, or if we are observing the rare behavior of a few opportunists or subset of the population.

Our analysis of inter-individual variation in *A. leachii* nocturnal activity showed no difference in the patterns of the eight marked individuals. This lack of variation suggests that individuals at our study site are adapting to the novel night-light niche similarly; however, three individuals were only detected once each, and our inferences into inter-individual trends are limited in general by sample size. We were able to conclusively determine the sex of six of eight *A. leachii*; cloacal scales are pronounced in mature males and ambiguous in females and subadult males (Lovern et al. 2004). We made no confirmed sightings of female anole activity in a set of 90 total observations, and it seems likely that nocturnal behavior in female *A. wattsi* and *A. leachii* is either nonexistent or very rare at this site. Therefore, this study suggests a possible sexual bias in the exploitation of the night-light niche. This is consistent with previous observations of nocturnal activity in the Anguilla Bank Anole (*A. gingivinus*; Powell and Henderson 1992). Further research would benefit from exploring this sexual bias in activity and should investigate what factors might drive sex-based differences in use of the night light niche.

To develop a more comprehensive understanding of the effects of light pollution, it will be important to consider how prevalent exploitation of the night-light niche is across species and contexts, and why individual species may vary in their use of this evolutionarily novel opportunity. Though *A. wattsi* is more abundant than *A. leachii* in Antigua (Kolbe et al. 2008), our study suggests that nocturnal activity is more common in *A. leachii*. Moreover, the limited available evidence suggests that *A. leachii* has been using artificial light sources for some time (Schwartz and Henderson 1991). The reasons for this are unclear, but the disparity may shed light on the traits valuable for taking advantage of nocturnal opportunities. *Anolis leachii* is larger than *A. wattsi* and thus could be a stronger competitor in any agonistic interactions with nocturnal species. Further, *A. leachii* typically occupies higher perches than does *A. wattsi* (Kolbe et al. 2008), a trait that coincides with a closer proximity to light sources that are most often located high on walls and ceilings. Perhaps *A. leachii* started to use the night-light niche when arthropod prey aggregated in front of them at light sources at the beginning of their natural diurnal activity.

Our observations of a single male *A. wattsi* exhibiting nocturnal foraging activity may be the result of idiosyncratic individual behavior. More nocturnal surveys are needed to better establish how prevalent this behavioral shift is for the species; however, with 78 *A. leachii* detections, our inferences are more robust for this species. Additionally, our observations of *A. leachii* using artificially lighted habitats are not isolated.

Individuals of the species shifted into the night-light niche at least as early as 1991 and likely before (Schwartz and Henderson 1991). We have also incidentally observed *A. leachii* nocturnal foraging behavior around artificial lights in other areas of Antigua away from the focal study area (e.g., Hodge's Bay and Piccadilly, Antigua). In each situation *A. leachii* were foraging on flying insects by artificial light sources, suggesting that the use of the night light niche by *A. leachii* could be widespread on Antigua.

The body of research documenting use of artificially lighted habitats by a variety of taxa continues to grow (Rich and Longcore 2006). Evidence is mounting that suggests humans are contributing to increasing nocturnality in wildlife (e.g., in mammals; Gaynor et al. 2018). As more ecological impacts become apparent (Gaston et al. 2014; Dominoni et al. 2016), investigating the fitness consequences of light at night will become increasingly important. Despite this, light at night remains understudied as a topic of regional conservation concern in the Caribbean. We suggest that future research should examine whether Caribbean species show an ability to exploit the night-light niche and how the use of this niche may result in downstream effects on species persistence and ecosystem function.

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