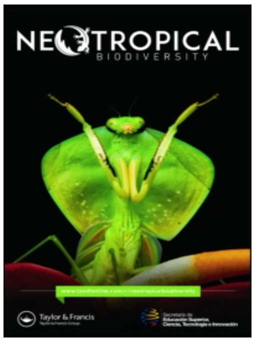

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No need for artificial light: nocturnal activity by a diurnal reptile under lunar light

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ABSTRACT

Species are commonly described as either diurnal or nocturnal, with rare reports of deviations outside their normal activity period. Observations of nocturnal activity by diurnal *Anolis* are limited to lizards utilizing anthropogenic light sources (night-light niche) to prolong their daily activity period. Here, we report nocturnal activity by *Anolis cristatellus* facilitated solely by natural moonlight and discuss implications for when this behavior would be recognized as common in the future. The identification of nocturnal activity in *Anolis* is particularly noteworthy given, in contrast to other taxa, our extensive knowledge of this study system which will allow for future ecological studies to better test hypotheses.

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Here we report observations of nocturnally active anole lizards under natural moonlight conditions from the Commonwealth of Dominica. These observations were made during 2019 while performing night surveys for alien *Osteopilus septentrionalis* in an area absent of anthropogenic light (15.561876, –61.458029 [1];). On 18 January, at 19:59, we observed a juvenile *Anolis cristatellus* predating on a fly (Dolichopodidae) immediately upon shining our light on the anole as it leapt from one grass blade onto another ahead of successful predation. However, the surprise of this first observation meant we could not photographically document this. On 16 April, at 20:40, we found an adult *A. cristatellus* predating on an adult *Eleutherodactylus martinicensis* (Figure 1). The anole was spotted on a PVC pipe with the frog partially inside its mouth. Documenting the event from a closer distance likely caused for the anole torelease its living prey. Both sightings occurred on the internal part of an abandoned plot consisting of overgrown, hurricane-damaged structures vegetated mainly by grass; trees are present as a single surrounding tree line (<7 m high). Adjacent plots are of similar disturbed nature, with the closest native undisturbed forest patch at >400 m (direct line).

Due to ecological and physiological trade-offs, species are generally described as diurnal or nocturnal. Deviations (when species are active outside their temporal niche under natural light conditions) are rarely observed in visually oriented species, with some exceptions from mammals [2], birds [3] and reptiles [4]. At night, in contrast to lunar light, several reptilian species, mainly *Anolis* lizards, have been observed to utilize artificial light (known as the night-light niche [5,6]). With >400 species, *Anolis* is an intensely studied model system for a wide scale of topics, ranging from ecology to invasive dispersal and adaptive radiation to genomic evolution [7–10]. Despite this extensive scientific attention, nocturnal behavior has only been reported in some cases [6,11,12], which were all facilitated by anthropogenic light sources. After a natural history literature assessment [13], to our knowledge, nocturnal activity of anoles facilitated by natural lunar light has not been reported.

These observations demonstrate energetic nocturnal activity, namely active predation and not merely looking for a sleeping perch after sunset. It is impossible to know whether our lights influenced these lizards, however, given only one person was present and that each predation event was observed directly on arrival, human disturbance (light and sound) was minimal. In our combined five years of fieldwork experience, these were the first occasions where an anole was observed other than asleep in an area absent from artificial light. Lastly, we note that the observed frog predation (attempt) by an anole is rarely reported, and only some cases are known from a small set of species; for an overview see Aguilar-López et al. [14].

Both nights were characterized by the absence of cloud cover and by strong lunar light conditions, both in waxing gibbous with 92.9% and 91.7% visibility, respectively (www.mooncalc.org); 100% equals full moon conditions. Data on moonlight intensity on Dominica are absent, though under ideal full-moon circumstances can reach 0.32 lux in the tropics [15],

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Figure 1. Nocturnal predation by an adult Puerto Rican Crested Anole (*Anolis cristatellus* Duméril & Bibron, 1837) on an adult *Eleutherodactylus martinicensis* on 16 April 2019 at 20:40.

and is among other factors dependent on latitude, time, air pollution, moon phase, cloud cover, and month of the year. Nocturnal temperature levels at this site are within the active range for *A. cristatellus* during summer months [16].

Diurnally active and visually oriented animals have light intensity thresholds that restrict their activity since, under lower levels of light, movement goes undetected. Few studies have measured physiological responses to (low) light conditions in anoles [15,17]. *Ex-situ*, Moore *et al*. [14] show that during nights with nocturnal light conditions (dim-to-full moonlight, 3.7×10^{-3} – 2.9×10^{-1} µW/cm^2) anoles demonstrate increased activity comparative to light-absent nights, which was moderate for *A. cristatellus* and higher for species inhabiting shade-rich habitats. Therefore, their data indeed suggest that lunar light conditions can facilitate nocturnal activity by diurnal anoles. Furthermore, in an *ex-situ* experiment focused on artificial light utilization, Thawley and Kolbe [18] recently found that nocturnal (thus prolonged) activity increases the fitness of *Anolis sagrei* through a higher reproductive output, without compromising offspring quality. Our observations suggest this higher fitness may not be limited to anoles that utilize artificial light; we recommend future *in-situ* studies into this relationship under lunar light. A better understanding of *Anolis* light restrictions under *in-situ* conditions will help to identify the precise range of light intensity anoles can utilize as well as the time period these species can be nocturnally active for per moon cycle.

In light of the extensive anole research, why has nocturnal activity under natural light conditions not been observed yet? One explanation is that the majority of anole research focuses on their diurnal activities through diurnal fieldwork, although genetics sampling is easier at night when anoles are asleep and easy to capture. Another explanation might come from the high association of anoles to trees and thus foliage cover [8], which would reduce or block moonlight. Indeed, our observations were from a grass-overgrown site lacking tree patches. A third explanation could be that the potential to utilize low-light conditions is restricted to a subset of anoles. Perry and Fisher [11] noted that most species observed to utilize the night-light niche are West Indian anoles; however, as no study aimed to assess this behavior throughout *Anolis*, and night-light niche data from non-West Indian anoles are increasing [19], our current knowledge is likely biased by increased research interest. A dedicated study into the extent of nocturnal activity throughout *Anolis*, as well as other reptilians, is recommended which, given thermal and visual limits/restrictions, could focus on lowland (sub) tropical regions and evenings around a full moon.

If more common, which anoles would exhibit nocturnal activity? Intuitively, shade-adapted species showed the highest activity under lunar light conditions *ex-situ* [15] but what about *in-situ*? Namely, shade-adapted species presumably are shaded from lunar light as *Anolis* sleeping perches depend on microhabitat choice [20]. Utilizing a minimal sample size, Moore et al. [15] found that the magnitude of nocturnal activity differs between ecomorphs, but not within. Species occupying less-shaded or open habitats are more likely to perceive the full intensity of lunar light. Moreover, such species likely experience thermal conditions that inhibit mid-day activity [8], which could have driven them to extend their daily activity period into the night. Future *in-situ* studies should focus on nocturnal activity difference concerning habitat and ecomorph types.

Exhibiting novel behavior or utilizing novel niches can give species an ecological advantage and increases species interactions. Besides facilitating predator avoidance [15], nocturnal activity can aid other behaviors like the predation reported here. While nocturnal activity may facilitate diurnal predator avoidance, it may also expose anoles to novel nocturnal predators. This could partially explain high anole predation by owls on Dominica [21] as well as predation by bats, besides their apparent ability to locate sleeping anoles [22]. From an invasive perspective, we note that the artificial night-light niche is utilized by many anole species with invasive populations [6,23,24]. However, whether this can be explained by a tendency to exhibit edificarian behavior [25] or optimize their ability to utilize lunar light should be addressed in future studies. Lastly, as invasive species tend to be generalist and highly adaptive species with broad niches [26–28], filling seemingly untaken niches would aid invasive success and establishment. Indeed, on Dominica, nocturnally active invasive *A. cristatellus*, that arrived around 2000 and competes with its native sister species [29,30], are presumed to fill an empty niche given the low number of nocturnally active herpetofauna species [27].

If recommended future surveys identify nocturnal behavior as wide-spread among *Anolis*, that would suggest the width of *Anolis* ecology and evolutionary adaptations are currently underestimated. The identification of nocturnal activity in *Anolis* is particularly intriguing given the vast literature and scientific interest into this study system. Contrarily to other taxa, this knowledge enables future studies to better test hypotheses both during *in-* and *ex-situ* experiments [17], and in nocturnal ecological studies on species interactions as have been widely studied under diurnal conditions [8].

Disclosure statement

No potential conflict of interest was reported by the authors.

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