The use of an artificial niche dimension by the introduced *Anolis cristatellus* (C. Duméril and Bibron, 1837) in the Caribbean lowlands of Costa Rica.

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Few animal species engage both in diurnal and nocturnal activities, or shift between the two (Abom *et al*., 2012; Fraser *et al*., 1993) because diel activity patterns normally are well established (Abom *et al*., 2012). Most animals have set activity times and as such species can be classified as diurnal, crepuscular, nocturnal, or cathemeral (Abom *et al*., 2012; Kronfeld-Schor & Dayan, 2003; Toms *et al*., 2022). Most lizards of Gekkota (geckos and pygopodoids) are nocturnal, however, the majority of other lizards predominantly are diurnal (Stark *et al*., 2020; Vidan *et al*., 2017; Vieira *et al*., 2020). Moreover, species of lizards excluding *Gekkota* that are active both diurnally and nocturnally are extremely rare, as are those that may shift from diurnally to at least partially nocturnality if conditions allow (Amadi *et al*., 2021), as has been found in some snakes (Abom *et al*., 2012).

Although the environmental factors associated with lizard nocturnal activity largely remain unknown (Vidan *et al*., 2017), it is known that activity levels of ectotherms, including lizards, primarily is correlated with availability of external heat sources (Afsar *et al*., 2018; Pianka & Vitt, 2006; Vidan *et al*., 2017; Underwood, 1992). As heliothermic organisms, diurnal lizards depend on sunlight and are active during the day; however, they sometimes can be active in the absence of this abiotic factor (Afsar *et al*., 2018; Nordberg & Schwarzkopf, 2019; Rose, 1981; Vieira *et al*., 2020). As a result, over 40 diurnal reptile species, particularly anole lizards (*Anolis* spp., Squamata: Dactyloidae), have expanded their niche from diurnal to nocturnal habits (e.g., Baxter-Gilbert *et al*., 2021), although these statements have in general been informed by anecdotal reports (Amadi *et al*., 2021; Baxter-Gilbert *et al*., 2021;

Maurer *et al*., 2019). The transition from diurnality to nocturnality generally occurs under particular conditions. Large lizards such as iguanas have thermal inertia that allows them to transition in their tropical ranges (Mora, 1986). Other species take advantage of the availability of additional food: for example, insects that are attracted to artificial lights (Owens & Lewis, 2018). Because lizards are ectotherms, nocturnal activity in the vicinity of artificial light comes with the requirement to cope with lower night-time temperatures due to the lack of external heat source (Gaston, 2019; Nordberg & Schwarzkopf, 2019; Vidan *et al*., 2017). As a result, this activity niche, often referred to as the night-light niche, is not exploited commonly (Amadi *et al*., 2020; Amadi *et al*., 2021; Gaynor *et al*., 2018). Besides, patterns of diel activity normally are fixed firmly to function most successively at the time of day when individuals are most likely to be active, as determined by eye morphology, intraspecific communication methods, and body coloration (Abom *et al*., 2012). These diel activity cycles are one of the key niche partitioning elements among lizard species (Pianka & Vitt, 2006); it therefore is rare to find species of lizards that are active both diurnally and nocturnally (Amadi *et al*., 2021; Gaynor *et al*., 2018). However, increased urbanization and the concomitant presence of artificial light at night (ALAN; Gaston *et al*., 2014) have facilitated the transition of several normally day-active lizard species to extend or even change their typical diurnal behavior patterns to extend into crepuscular and even nocturnal activity (Maurer *et al*., 2019; Perry *et al*., 2008). This is notably true for anoles, whose dominant sense for prey acquisition is sight (Maurer *et al*., 2019), and particularly for introduced species, where 14 out of 20 known introduced species have been observed using ALAN (Thawley & Kolbe, 2020).

Anoles are one of the most species rich of all the lizard groups (Pianka & Vitt, 2006; Pyron *et al*., 2013; but see Nicholson *et al*., 2012). Interspecific competition among species of anoles is avoided by using distinct microhabitats within their geographic ranges; the use of distinct microhabitats within ecosystems results over evolutionary time in distinct and predictable evolutionary trajectories (Crandella *et al*., 2014; Losos, 2009). This group of lizards therefore have been hypothesized as recurrently evolving into occupancy of a distinct set of niches (Losos *et al*., 2003) wherein each species is associated with a specific suite of morphological and ecological characteristics (Mora & Escobar-Anleu, 2017; Walguarnery *et al*., 2012).

Anolis cristatellus (Dactyloidae: Squamata: Reptilia) is a species native to Puerto Rico and the

British Virgin Islands; in Costa Rica is a highly adaptable invasive species that is tolerant of habitat alteration (Hall & Warner, 2018; Kolbe *et al*., 2021; Thawley *et al*., 2019). It initially was found in Costa Rica on the giant fig trees of Parque Vargas, Port of Limón (Savage, 2002), but now is commonly found in city parks, roadside vegetation, and within homes and other structures, throughout much of the southern Atlantic coastal plain region of Costa Rica (Leenders, 2019) as well as in a few other localities in Limón and Cartago provinces (Savage, 2002). It is a diurnal species (Garber, 1978) that perches on the lower trunks of trees, on the ground, and on walls and rafters of wooden structures, where it sits and waits for prey, principally arthropods, moving along the ground (Leenders, 2019; Savage, 2002). *Anolis cristatellus* appears to be restricted to open habitats (Garber, 1978): in Cahuita, also in Limón, for example, only a small creek separates the town from a national park (Parque Nacional Cahuita; creek at ca. 9.7363889°N, 82.83917°W), but the natural forest milieu appears to constitute an impenetrable—or certainly unsuitable—ecological matrix for this species.

Anolis cristatellus is a moderate-sized anole (205 mm total length; tail ca. 60 to 65% of total length; Savage, 2002). They are dull brown with several transverse dark bars in males and overlapping diamond-shaped blotches in many females (Savage, 2002). This species is easily recognized because they have a distinct caudal crest, more developed in males, and the dewlap is greenish yellow with the free margin of burnt orange to reddish, smaller in females (Savage, 2002).

Artificial light at night is one of the many consequences of contemporary human development, and although its impacts on biodiversity as a component of anthropogenic global change is increasingly being recognized, they remain poorly understood (Maurer *et al*., 2019). Animals such as anoles that use sight as a primary sense in prey acquisition have as a result obtained new opportunities to exploit the night-light niche (Kolbe *et al*., 2021; Maurer *et al*., 2019). At least seventeen species of anoles have been documented using ALAN (Maurer *et al*. 2019; Perry *et al*., 2008). However, the ecological consequences of this nocturnal activity by anoles, and other organisms, also largely remain unknown (Maurer *et al*., 2019; Rutschmann *et al*., 2021). In laboratory conditions, brown anoles (*Anolis sagrei*) exposed to ALAN increased growth and did not suffer apparent negative consequences (Thawley & Kolbe, 2020). Individuals exposed to ALAN developed earlier egg-laying, probably by mimicking a longer photoperiod, and increased reproductive output without reducing offspring quality and likely increasing fitness (Thawley & Kolbe, 2020). *Anolis cristatellus* normally exhibits diurnal behaviour; here we report its nocturnal activity in Costa Rica under ALAN.

On 06 March 2018 at 2134 h we observed a large male *Anolis cristatellus* perched close to a white, fluorescent light source (Figure 1). This male was hunting in the inside upper part of the outside dining room of Las Veraneras hotel, in Manzanillo, Limón (9.630276° N, 82.660276°W; 8 m asl). The individual remained at its perch hunting insects until at least 2300 h, when we left the site. We visited this site again on 27 June 2019 and observed another individual in the same location. On both occasions we saw individuals of this species in the vicinity of the dining room during the day, but not in the upper part where the individuals observed at night on the two recorded occasions were located.

An increase in the prevalence of ALAN is an important component of global environmental

Figure 1. An adult male *Anolis cristatellus* perched close to a white, fluorescent light source, nocturnally foraging for insects at an open dining room, Manzanillo, Limón, Costa Rica. Photo: José M. Mora.

Figura 1. Un macho adulto de *Anolis cristatellus* posado cerca de una fuente de luz fluorescente blanca, en busca de insectos durante la noche en un comedor abierto, Manzanillo, Limón, Costa Rica. Foto: José M. Mora.

change, however, its biological impacts only now are beginning to be recognized. Artificial lighting attracts and repels animals differentially according to each particular taxonomic group's ecological preferences (Mora *et al*., 2018). ALAN exposition may negatively affect a variety of organisms by means of disrupting key functions such as physiology, growth, stress, and reproduction, thereby resulting in adverse conditions for many species in urban areas (e.g. Gaston *et al*., 2015; Ouyang *et al*., 2017; Ouyang *et al*., 2018). However, it also may be favourable to other species, such as brown anoles, although those results are derived from laboratory conditions (Thawley & Kolbe, 2019). ALAN as part of the urbanization process drastically transforms the environment, and can create new habitats with different elements and dynamics that opportunistically can be leveraged by certain species (Badillo-Saldaña *et al*., 2016; McKinney, 2006; Perry *et al*., 2008). Lizards will adapt to such changes depending on whether the species under consideration are negatively impacted or whether they have the behavioural flexibility to exploit novel environmental conditions (Amadi *et al*., 2020).

Several reptile species, among many other organisms, have expanded nocturnal foraging in the presence of ALAN (Garber, 1978; Rydell, 1992; Thawley & Kolbe, 2020). ALAN has caused diurnal lizards adapted to living in urban areas to alter their diel cycles (Perry *et al*., 2008; Powell, 2015). Nocturnal activity facilitated by ALAN has been reported for several *Anolis* species (e.g. Badillo-Saldaña *et al*., 2016; Brown & Arrivillaga, 2017; Thawley & Kolbe, 2020). It is possible that anoles as well as other organisms could be resistant to at least some of the negative effects of ALAN, and even could take advantage of the novel niche space ALAN creates (Thawley & Kolbe, 2020). Most reports on anole nocturnal activity are from Tropical environments, most likely because the ecological and physiological characteristics such as the optimal body temperatures typical of these lizards allow them to exploit available resources depending on the ambient temperature, which is less variable from day to night in the tropics than in temperate regions (Badillo-Saldaña *et al*., 2016; Janzen, 1967; Medina *et al*., 2016). Tropical temperatures enable anoles to maintain high body temperatures both day and night allowing diurnal species become cathemeral resulting in changes in movements patterns (Abom *et al*., 2012).

Many species of lizards are insectivorous, and insects are influenced strongly by lighting (Owens & Lewis, 2018). Nocturnal activity by diurnal lizards may allow for maintenance and importantly, expansion of territories, as well as opportunities for courtship and reproduction and avoidance of competition and predation (Gaston, 2019; Kolbe *et al*., 2021; Maurer *et al*., 2019; Rich & Longcore, 2006). It has been hypothesized that nocturnal exposure and movement by spotted turtles (*Clemmys guttata*) provide them with increased time for foraging or mate-seeking, investing daytime hours for basking (Toms *et al*., 2022). Night-time also can be used for basking, as shown by Krefft's river turtles (*Emydura maquarii krefftii*) in Australia (Nordberg & McKnight, 2020). For most ectotherm terrestrial animals in tropical and desert areas, the principal thermal challenge is not to attain high body temperatures but rather to stay cool (Kearney *et al*., 2009). This means that in the tropics, diurnal, sight-dependent species, such as anoles, potentially could "compensate" for the hours of activity precluded by excessively high temperatures with periods of nocturnal activity within more suitable temperature ranges when ALAN is provided. This could particularly be the case in lizard species adapted to live in urban areas such as *Anolis cristatellus*. This species perches on broader, smoother, artificial substrates such as concrete walls and metal fences rather than the trunks of trees found in natural habitats (for Puerto Rico, see Tyler *et al*., 2016); preference for broad substrates accordingly resulted in niche expansion for this species in Miami, Florida (Battles *et al*., 2018).

Some diurnal lizards that are active under ALAN conditions potentially and eventually could be active in such areas under conditions absent artificial light if temperature allows activity. It was reported that *Anolis cristatellus* may be active under moonlight (on Dominica: Brisbane & van den Burg, 2020). We hypothesize that presence of artificial light is the first stimulus for nocturnal activity on the part of some lizard species, given the opportunity for extended foraging and consequent increased energy acquisition (Dwyer *et al*., 2013). They then would transition to nocturnal activity in the presence of moonlight if temperature and other environmental conditions allow it. Several reports, albeit isolated, have reported nocturnal or crepuscular activity in lizard species and other reptiles otherwise characterized as diurnal (Arenas-Moreno *et al*., 2018; Arenas-Moreno *et al*., 2021; Lara-Resendiz, 2020; Nordberg & McKnight, 2020; Rutschmann *et al*., 2021; Toms *et al*., 2022). Warm environments as are the Caribbean lowlands of Costa Rica may allow *Anolis cristatellus* to be active at night because absence of an external heat source is not a limiting factor. It has been shown that anoles are behaviourally capable of exploiting novel resources, and many species have been observed foraging nocturnally under ALAN in urbanized areas where they are invasive (e.g. Badillo-Saldaña *et al*., 2016; Brown & Arrivillaga, 2017; Kolbe *et al*., 2016;

Lapiedra *et al*., 2017; Maurer *et al*., 2019; Perry *et al*., 2008; Thawley & Kolbe, 2020; Winchell *et al*., 2018). Invasiveness in some reptiles may depend on their ability to exploit the night-light niche (Perry *et al*., 2008; Thawley & Kolbe, 2020). Negative and positive impacts of ALAN may play a determining role selecting which species invade and exploit urban environments (Thawley & Kolbe, 2020).

Buffering for the hours of activity precluded by excessively high temperatures with periods of nocturnal activity within more suitable temperature ranges when ALAN is provided could be an alternative for tropical lizards affected by warmer conditions due to climate change. In addition, warmer nocturnal temperatures can advance reproduction timing and increase offspring quality, as was shown in the Otago gecko (*Woodworthia* "Otago/Southland"; Moore *et al*., 2020). However, increases in nocturnal temperatures may provide body operating temperatures leading to increased individual performance but reducing optimal resting time and raising energetic costs of rest (Rutschmann *et al*., 2021). ALAN may alter activity towards night time in environments where daily temperatures exceed critical maximum temperatures (Lara Resendiz, 2019; Nordberg & Schwarzkopf, 2019). However, these changes may have consequences over community and ecosystem structure by their effects on dispersal strategies, population dynamics, and intra- and interspecific interactions (Toms *et al*., 2022). The plasticity evidenced by *Anolis cristatellus* in expanding its foraging niche to a nocturnal milieu points to a potentially important suite of behavioural characters that may enable this and other species equipped with such behavioural flexibility to weather impending increases in environmental temperature regimes.

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