

Research



Cite this article: Thawley CJ, Kolbe JJ. 2020 Artificial light at night increases growth and reproductive output in *Anolis* lizards. *Proc. R. Soc. B* **287**: 20191682. <http://dx.doi.org/10.1098/rspb.2019.1682>

Received: 17 July 2019

Accepted: 18 December 2019

Subject Category:

Global change and conservation

Subject Areas:

physiology, ecology

Keywords:

urbanization, lizard, artificial light at night, invasive species, life history, reproduction

Author for correspondence:

Christopher J. Thawley

e-mail: cthawley@gmail.com

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4800069>.

Artificial light at night increases growth and reproductive output in *Anolis* lizards

Christopher J. Thawley and Jason J. Kolbe

Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881, USA

CJT, 0000-0002-6040-2613

Since the invention of electric lighting, artificial light at night (ALAN) has become a defining, and evolutionary novel, feature of human-altered environments especially in cities. ALAN imposes negative impacts on many organisms, including disrupting endocrine function, metabolism, and reproduction. However, we do not know how generalized these impacts are across taxa that exploit urban environments. We exposed brown anole lizards, an abundant and invasive urban exploiter, to relevant levels of ALAN in the laboratory and assessed effects on growth and reproduction at the start of the breeding season. Male and female anoles exposed to ALAN increased growth and did not suffer increased levels of corticosterone. ALAN exposure induced earlier egg-laying, likely by mimicking a longer photoperiod, and increased reproductive output without reducing offspring quality. These increases in growth and reproduction should increase fitness. Anoles, and potentially other taxa, may be resistant to some negative effects of ALAN and able to take advantage of the novel niche space ALAN creates. ALAN and both its negative and positive impacts may play a crucial role in determining which species invade and exploit urban environments.

1. Background

Urbanization is radically transforming landscapes across the planet. Cities house the majority of the world's population and produce greater than 75% of its gross domestic product (GDP) and carbon emissions [1]. Humans are increasingly moving to urban areas, which are predicted to grow in size and impact over the next century [2]. Many species decline in abundance or are absent from urban habitats, whereas others persist in and often exploit these habitats, showing changes in life history, physiology, and behaviour [3,4]. Urban habitats are altered from natural ones in many ways, including increased temperatures due to the urban heat island effect [5], altered structural habitat [6,7], and the presence of artificial light at night (ALAN) [8].

ALAN is associated most strongly with the use of electrical lighting in human population centres and transportation networks (e.g. roads, railways), and its extent and intensity are growing annually [8,9]. This effect is strongest in urban areas, where the top 125 urban centres in the USA account for only 2% of land area but create over one third of the total light on the landscape [10]. In affected habitats, ALAN is an evolutionary novel environmental condition, fundamentally changing the predictable photic cycles of day and night from their historical baselines [8,11].

This novel condition has a variety of effects on organisms exposed to ALAN [12,13]. ALAN has direct physiological impacts, such as altering the melatonin production of affected organisms [14]. Physiological costs can include disruption of endocrine function, increased stress hormone levels, changes in energy expenditure, and altered immune function [15–17]. ALAN can also facilitate indirect ecological costs, including increasing vulnerability to predators [18,19]. However, ALAN can have positive impacts for species capable of exploiting the novel conditions it creates. For instance, in nocturnally foraging taxa, such as spiders and bats, and even some diurnally active species, ALAN

offers the opportunity for extended foraging and increased energy acquisition [20–22]. Both the positive and negative facets of ALAN impact key organismal functions and are likely to affect fitness [23,24].

Impacts of ALAN on fitness may be especially likely when reproduction is affected. Exposure to ALAN is known to disrupt reproduction, including advancing reproductive timing, which could lead to maladaptation in the case of phenological mismatch with food sources [23,25,26]. However, not all reproductive impacts of ALAN are negative, as some birds exposed to ALAN shift their phenology to begin laying eggs earlier and have enhanced mating opportunities [27]. These observed shifts in reproduction may be due to the potential for ALAN to mimic conditions of longer daylengths or photoperiods, which control reproduction in some animals, including birds [26,28] and lizards [29–31]. Photoperiod is a key environmental determinant of onset of reproduction and regulation of reproductive cycles in seasonally breeding animals and plants [32–34]. Effects of ALAN on reproduction can also interact with other organismal systems. For instance, breeding birds exposed to white ALAN had higher baseline corticosterone (CORT) levels than those exposed to controls [35]. While the potential for effects of ALAN on reproduction and fitness is high, our understanding of these impacts has generally been limited taxonomically to work in birds and mammals [13,17].

Anole lizards are an ideal group in which to study the impacts of ALAN on reproduction in reptiles. Lizards, including anoles, commonly exploit urban habitats where ALAN is the strongest [36,37]. An extensive body of research on the physiology of anoles has laid a strong foundation for understanding the impacts of ALAN on anole reproduction. Early experiments showed that altered photoperiods, including constant lighting, affect reproductive cycling and onset of reproduction in green anoles (*Anolis carolinensis*) in the laboratory [31,38]. However, this work showed stronger effects of temperature on reproduction and did not disentangle the effects of these two factors. In anoles, light at night impacts the production of melatonin, which plays an important role in reproduction in *A. carolinensis* [39,40]. However, anoles show higher resistance to impacts of ALAN on melatonin than other vertebrates [40,41], suggesting that the impacts of light at night on this group may differ from those previously observed in birds and mammals.

Brown anoles (*Anolis sagrei*) are frequent invaders of highly urbanized habitats where sources of direct ALAN (e.g. streetlighting, landscaping lights) are common, and they are exposed to ALAN at perches used for sleeping [42] (see the electronic supplementary material). Previous observational studies of brown anoles have suggested that photoperiod is linked to onset of reproduction in this species [43,44]. However, it remains unclear whether ALAN alone alters reproduction in anoles, and if so, how. We exposed brown anoles to both normal photoperiods and ALAN in the laboratory. We predicted that exposure to ALAN would serve as a stressor for lizards, decreasing growth and body condition and leading to elevated baseline levels of CORT, the primary stress hormone in reptiles. Given that ALAN can mimic extended photoperiods, we predicted that females exposed to ALAN would begin egg-laying earlier than those exposed to a normal photoperiod. We also predicted that ALAN exposure would reduce overall reproductive output, including number of eggs laid, frequency of egg-laying, and total egg mass produced. We predicted that mothers exposed

to ALAN would produce poorer quality eggs with reduced hatching success that would develop into smaller hatchlings in poorer condition.

2. Methods

In February 2017, we captured invasive brown anoles ($n_f = 32$, $n_m = 32$) via noose from a natural forest habitat remnant within the Miami urban matrix (25.65988, –80.28164; WGS84) prior to onset of egg-laying [41]. This area was exposed to skyglow from Miami but devoid of direct artificial lighting, and anoles sleeping at this site experience very low levels of nocturnal illumination (0.0–0.1 lux; electronic supplementary material). Anoles were transported to the University of Rhode Island and housed in a climate-controlled room. Male and female lizards were paired randomly in cages containing terrarium liners, natural perches, plastic plants, and small plastic pots with moistened coconut husk for egg-laying. Room temperature cycled daily between 22.5 (night) and 27.8°C (day). Two automated humidifiers maintained relative humidity at 55%, and cages were misted twice daily during which nesting pots were moistened as needed. Pairs of anoles were fed nine crickets dusted with vitamin and mineral powder three times weekly. Lizard health was monitored daily, and cages were rotated on shelves biweekly within treatments.

(a) Light treatments

Room lights were initially set to a 11.75 light:12.25 dark cycle replicating the Miami photoperiod, and daylength was updated in 15-min intervals throughout the experiment to track conditions in Miami. All cages were lit from above with UV light during daytime hours. At night, the room was divided by a heavy black plastic tarp sealed with tape which prevented light from either side from reaching the other. Half of the lizard pairs were randomly assigned to each side of the room, and neither sex differed in snout–vent length (SVL) with treatment (all $p > 0.11$). Lizards on one side of the room experienced the ‘dark at night’ (DAN) treatment, with extremely low light levels (≤ 0.1 lux; TES 1332A Digital Lux Meter) when room lights were off and no exposure to ALAN. Lizards on the other side of the room were exposed to the ALAN treatment. During times when room and UV lights were off, these lizards were exposed to LED lighting (3000 K; Lighting EVER; electronic supplementary material, figure S2) from one side. LED lights were positioned ≈ 1.5 m from cages and did not affect cage temperature. Light intensity at points in front of cages ranged from 23 to 44 lux. These levels are comparable to those at perches available to anoles within 4 m of landscaping lights that are common in urban areas (electronic supplementary material, figures S3 and S4). However, as cages contained extensive plastic foliage, lizards likely experienced much lower light intensities because most perch sites were not exposed to direct ALAN.

This treatment simulated novel exposure to the colour temperature and directional nature of landscape lighting common in the Miami area from sunset to sunrise. The treatment created a range of ecologically relevant ALAN conditions in each cage, from high levels experienced when foraging directly adjacent to lights, a common behaviour in anoles ([45–47]; electronic supplementary material, figure S4), to lower levels when perch sites were obscured by cover or foliage. Anoles in the Miami area experience significantly elevated light levels when sleeping in habitats such as urban parks when compared to the low levels experienced by lizards sleeping at our collection site ($W = 1$, $p < 0.0001$). Anoles foraging for insects within several metres of light sources in urban areas are likely exposed to much higher light intensities that overlap with those in our ALAN treatment (electronic supplementary material, figures S3 and S4).

(b) Morphology

We measured the SVL (to 1.0 mm) and body mass (to 0.01 g) of each lizard at capture and at two-week intervals until the end of the experiment. SVL was measured by one observer (CJT) with a ruler. We used standardized residuals from an ordinary least-squares regression of ln-transformed body mass on ln-transformed SVL conducted on females, males, and hatchlings separately as indices of body condition [48].

(c) Corticosterone

To assess levels of CORT, we took 15 µl blood samples from the post-orbital sinus of lizards using heparinized micro-capillary tubes. All samples were taken within 3 min (78.8 ± 2.6 s.e. seconds) of entering each anole's cage to reduce the chance of handling impacting plasma CORT levels [49,50]. Blood samples were taken from female anoles on the final day of the experiment and from male lizards six days prior to avoid stress from repeated captures in cages. To ensure that circadian rhythms in CORT levels did not influence our conclusions, blood samples were taken serially in one period each day (93 min, males; 73 min, females), and sampling alternated between treatment groups to prevent bias. Time to bleed and time of day were initially included as covariates in our analysis, but did not affect CORT (all $p > 0.32$) and were not included in the final model.

Blood samples were kept on ice until centrifuging, and plasma was stored at -20°C until quantification. CORT was quantified using a commercially available enzyme immunoassay kit. The kit was validated for use in *A. sagrei* by assessing parallelism and quantitative recovery (electronic supplementary material, S1). Plasma was diluted by 90% with assay buffer so that CORT concentrations fell within the detectable range of the assay's standard curve. We ran each sample in duplicate. The mean intraassay coefficient of variation within the kits was 3.16% (2.59–3.72%). The interassay coefficient of variation (4.12%) was calculated using control samples provided with the kits run on both plates used in this study.

(d) Reproductive output

Nesting pots were checked for eggs each day. Upon discovery, eggs were cleaned of debris, and wet mass was measured to the nearest 0.1 mg. Maximum length and width of eggs were measured to the nearest 0.1 mm using dial calipers (Swiss Precision Instruments). Up to the first four eggs produced by each female were frozen until the end of the experiment. Eggs were dried for 24 h at 60°C in a convection oven. Egg contents were separated from the shell. Egg dry mass and content mass were measured to the nearest 0.1 mg, and water content as a percentage of the initial wet egg mass was calculated. We incubated eggs not used to determine egg contents ($n = 51$) in an incubator set to a constant 29°C . Eggs were placed in glass jars filled with equal masses of vermiculite and distilled water. Jars were sealed with plastic wrap and rubber bands to reduce moisture loss. Every two weeks lost water was replaced as needed, and eggs were rotated between incubator shelves. Jars were checked daily for new hatchlings whose SVL (to the nearest 0.5 mm) and body mass (to the nearest 0.1 mg) were measured.

(e) Statistical analysis

We assessed impacts of ALAN on growth as change in SVL and body condition using linear models including ALAN treatment, sex, initial SVL, and initial body condition as predictors. Initial SVL and body condition were scaled and centred separately for each sex. Post hoc tests to determine effects of ALAN on each sex were conducted using the *emmeans* package [51]. We assessed whether lizards changed in body condition using

separate paired t-tests for each sex. We assessed whether ALAN affected levels of CORT in plasma using a linear model with ALAN, sex, SVL, and body condition as predictors. CORT was natural log-transformed, and SVL and body condition were scaled and centred separately for males and females.

We tested whether ALAN affected onset of reproduction in females (day of laying first egg) using survival analysis as implemented in the *survival* [52] and *flexsurv* [53] packages. Our starting model included ALAN and its interaction with initial SVL as well as initial body condition, but we excluded the ALAN*SVL interaction from our final model (likelihood ratio test (LRT); $\chi^2_1 = 1.06$, $p = 0.30$).

We tested for impacts of ALAN on the number of eggs and total egg mass produced by mothers over the course of the experiment using linear models including the interaction between ALAN treatment and initial SVL and initial body condition as a covariate. We assessed whether the proportion of females laying eggs during the experiment varied with ALAN exposure using a χ^2 -test with p -value determined via Monte Carlo simulation. We tested for effects of ALAN on the interval (in days) between eggs laid using a linear mixed model implemented in the *lme4* package [54] with ALAN as a fixed factor, a random effect for mother, individual egg mass, Julian day, and SVL of mother as covariates, and the interaction between mother's SVL and ALAN ($n = 130$). Interval between egg-laying was natural log-transformed.

We tested for impacts of ALAN on wet mass, length, and width of eggs ($n = 162$) using linear mixed models with ALAN as a fixed factor, a random effect for mother, Julian day, SVL of mother, and mother's body condition as covariates. Values for SVL and body condition of mother for each egg were taken from the most recent measurement prior to egg production. We tested for impacts of ALAN on egg dry mass, content mass, and water content ($n = 101$) using the same model structure. We assessed whether SVL of females when producing their first egg differed with ALAN exposure and whether the first eggs produced by each mother differed in their morphology (wet mass, length, width, dry mass, or water content) with ALAN exposure of the mother. These models used covariates that were significant predictors of each response variable in analyses using full datasets.

We assessed whether ALAN affected the incubation time of eggs to hatching, size, and body condition of hatchlings using linear mixed models with ALAN as a fixed factor, a random effect for mother, and egg mass, mother's SVL, and Julian day as covariates. We assessed whether the proportion of mothers for which all eggs hatched successfully varied with ALAN exposure using a one-tailed χ^2 -test with p -value determined via Monte Carlo simulation (20 000 replicates). In all models, interaction terms were removed from final models if they were not significant predictors. For mixed models, covariates including SVL, Julian day, and egg mass were centred and scaled to aid model convergence. All analyses were conducted in R [55]. Scripts and details of analyses are available in the electronic supplementary material (S3).

3. Results

Lizards exposed to ALAN grew more than those in a normal light–dark cycle ($\beta_{\text{ALAN}} = 0.731 \pm 0.201$, $p < 0.001$), and post hoc tests showed that ALAN had a significant effect on both sexes (both $p < 0.004$; figure 1). Females in artificial light grew 1.8 times more than their counterparts in the DAN treatment, while males grew 1.2 times more. As expected for logistic growth of lizards, both males and females that were smaller at the start of the experiment grew more ($\beta_{\text{SVL}} = -0.673 \pm 0.102$, $p < 0.001$). ALAN did not affect

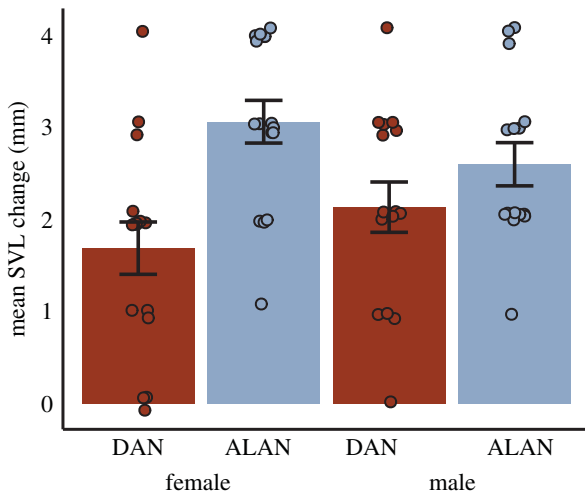


Figure 1. Means of growth in SVL are higher in ALAN (light blue) than DAN (dark red) treatments for both female and male anoles. Error bars ± 1 s.e. (Online version in colour.)

change in body condition ($\beta_{\text{ALAN}} = 0.045 \pm 0.185$, $p = 0.81$). Female lizards increased in body condition during the experiment ($t_{31} = -8.177$, $p < 0.001$), likely due to onset of breeding season, but male lizards did not change in body condition ($t_{29} = 0.167$, $p = 0.87$). ALAN exposure did not affect levels of CORT in plasma of either sex ($p = 0.11$), and females showed higher levels of CORT than males ($\beta_{\delta} = -0.884 \pm 0.190$, $p < 0.001$).

Females exposed to ALAN laid eggs earlier than females in the DAN treatment ($\beta_{\text{ALAN}} = -0.530 \pm 0.157$, $p < 0.001$; figure 2). As a result, ALAN females of average SVL are predicted to lay eggs an average of 10.76 days earlier than those in the DAN treatment, resulting in an average increase of ≈ 1.5 eggs/season due to the effect of ALAN on onset of reproduction. Larger females laid eggs earlier ($\beta_{\text{SVL}} = -0.137 \pm 0.045$, $p = 0.002$), but body condition did not affect onset of egg-laying ($\beta_{\text{BC}} = -0.084 \pm 0.094$, $p = 0.37$). Total eggs produced and total egg mass were highly correlated ($r = 0.99$) and were both impacted similarly by an interaction between exposure to ALAN and body size ($\beta_{\text{ALAN} \times \text{SVL}} = -1.135 \pm 0.451$, $p = 0.018$; $\beta_{\text{ALAN} \times \text{SVL}} = -0.180 \pm 0.078$, $p = 0.029$, respectively; figure 3). Smaller females (less than ≈ 42 mm SVL) exposed to ALAN produced nearly double the number of eggs and total egg mass predicted for smaller females exposed to a normal photoperiod. The proportion of females laying eggs did not vary between treatments ($\chi^2 = 2.133$, $p = 0.487$). Interval between eggs laid varied interactively based on female size and exposure to ALAN ($\beta_{\text{ALAN} \times \text{SVL}} = 0.171 \pm 0.083$, $p = 0.046$). Smaller females in ALAN treatments laid eggs more frequently (i.e. shorter intervals) than smaller females exposed to a normal photoperiod (figure 4).

Wet mass of eggs did not differ with mother's exposure to ALAN, Julian day, or body condition (all $p > 0.15$), but larger females did lay more massive eggs ($\beta_{\text{SVL}} = 0.005 \pm 0.002$, $p = 0.030$). Eggs from mothers exposed to ALAN were shorter ($\beta_{\text{ALAN}} = -0.365 \pm 0.118$, $p = 0.003$), but width did not differ with mother's exposure to ALAN ($p = 0.44$). Eggs from mothers exposed to ALAN had lower content mass ($\beta_{\text{ALAN}} = -0.002 \pm 0.001$, $p = 0.033$), averaging 5.8% lower in mass, but did not differ in dry mass or water content (all $p > 0.09$). The first eggs produced by each mother did not differ in wet mass, length, width, dry mass, or water content with mothers'

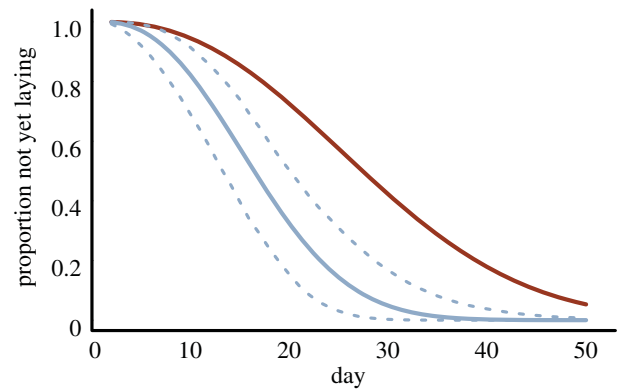


Figure 2. Females in ALAN treatments (light blue) lay eggs earlier than females exposed to a normal photoperiod, (DAN; dark red; dashed lines represent 95% CI). Curves are predicted values for individuals with mean SVL and body condition from survival model. (Online version in colour.)

exposure to ALAN (all $p > 0.068$), and body size of females when they laid their first egg did not differ between ALAN and DAN treatments ($p = 0.14$).

All incubated eggs ($n = 22$) from females ($n = 8$) in the DAN treatment hatched successfully. Only 79% of eggs ($n = 29$) from females ($n = 11$) in the ALAN treatment hatched successfully. However, these results are driven by one female that failed to hatch any eggs ($n = 3$). While eggs from four different mothers in the ALAN treatment failed to hatch, the proportion of mothers hatching all eggs successfully from both treatments did not differ ($\chi^2_1 = 3.685$, $p = 0.053$). Incubation time of hatchlings, hatchling size, and body condition were unaffected by exposure of mothers to ALAN (all $p > 0.42$).

4. Discussion

Exposure to ALAN negatively impacts a variety of organisms, disrupting key functions including physiology, growth, stress, and reproduction, and is an adverse condition for many species in urban areas [12,13,17,56]. In contrast to previous work, we found that exposure to ALAN in brown anoles maintained in a laboratory environment resulted in increased growth and reproductive output with little indication of costs.

Both male and female anoles exposed to ALAN grew more in the laboratory. Exposure to extended photoperiods (18 L: 6 D), but not ALAN, has been shown to increase growth and appetite in males of the congener, *A. carolinensis* [38]. It is possible that exposure to ALAN functions similarly and could have allowed anoles to make better use of available food resources, supporting higher growth (see below). Daily growth rates of females exposed to ALAN were ≈ 1.8 times those in the DAN treatment, suggesting that these increases are biologically significant. In brown anoles, larger size is linked to intraspecific competitive dominance [57], higher endurance [58], and greater reproductive output [59]. As a result, anoles that can make use of ALAN may experience increased fitness.

We did not detect costs of exposure to ALAN in adult anoles, as both body condition and baseline CORT levels were unaffected by treatment. The lack of effect of ALAN on CORT levels is surprising, as exposure to ALAN has been shown to alter glucocorticoid levels in other organisms

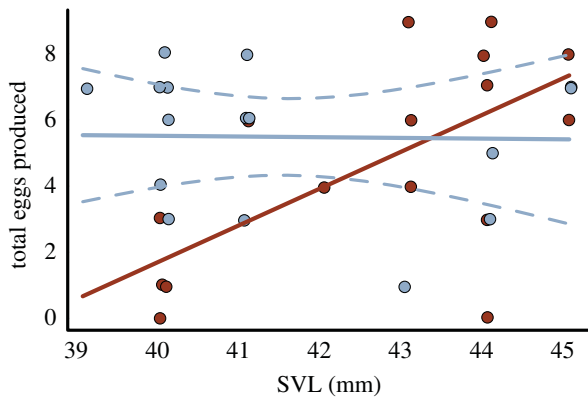


Figure 3. Under normal photoperiod (DAN; dark red), number of eggs produced increased with female size. However, smaller females exposed to ALAN (light blue) produced elevated numbers of eggs (dashed lines represent 95% CI). (Online version in colour.)

[17]. We hypothesized that CORT increases due to ALAN might cause increased investment in maintenance and decreases in energy investment in reproduction and growth [60]. However, we reject this hypothesis as anoles exposed to ALAN seemed to have similar energy reserves (as reflected in body condition) and greater growth and reproduction which both require energetic investment. It is also possible that anoles experienced costs of ALAN exposure in relevant physiological areas that we did not assess, such as immune function, for which costs of ALAN are present in many taxa [15,24,61] or cognitive abilities [62]. Future work addressing the potential costs of ALAN in other organismal systems would be beneficial.

Female anoles exposed to ALAN began laying eggs significantly earlier on average in the spring than females exposed to DAN. Research in avian species has shown that birds using urban habitats may breed earlier than their rural counterparts, and this difference may be due to exposure to ALAN among other factors [26,27,63]. Early field studies suggested that onset of reproduction in many anole species may be driven by a combination of light and temperature cues [64,65]. More recent observational studies in brown anoles also suggest that photoperiod may be linked to onset of reproduction, but are unable to disentangle effects of temperature from light cues as they are strongly correlated [43,44]. Early laboratory work in *A. carolinensis* showed that altering melatonin, pineal function, and photoperiod can affect onset of egg development and reproduction [31,66,67], but did not use ALAN treatment. Experiments in other lizard species with constant lighting have subjected animals to very high light intensities and confounded light and heat [68,69]. To our knowledge, this study is the first to show that ALAN levels similar to those experienced by lizards foraging in urban areas can accelerate onset of reproduction in lizards independently of heat. It seems likely that ALAN exposure simulates longer photoperiods, resulting in female anoles beginning egg production earlier in the spring. Potential effects of ALAN-extended photoperiods at the end of the reproductive season in the fall are unknown, though previous work suggests these are likely as well [66].

Anoles exposed to ALAN were predicted to begin laying eggs an average of ≈ 11 days earlier than females in the DAN treatment, contributing to their significantly higher reproductive output, and this effect was consistent across female size.

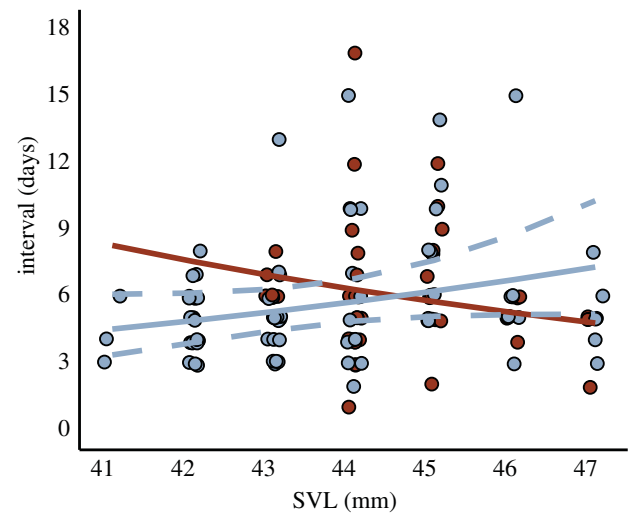


Figure 4. Smaller females exposed to ALAN (light blue) laid eggs significantly more frequently (lower interval) than similarly sized females under normal photoperiod (DAN; dark red; dashed lines represent 95% CI). Outlier with interval = 26 not shown. (Online version in colour.)

However, total egg output and total egg mass increased in smaller females only when exposed to ALAN; these lizards produced twice the eggs laid by their counterparts in the normal photoperiod (figure 3). In the DAN treatment, egg output increased with mother's size, a pattern observed previously in brown anoles [59], with smaller females producing a mean of 2–3 eggs and larger females producing a mean of six eggs. In the ALAN treatment, however, smaller females produced similar numbers of eggs to the largest females, averaging 5–6 eggs produced over the experiment. This output was accomplished in part by smaller females in the ALAN treatment producing eggs at a significantly higher rate (i.e. a shorter interval) than anoles exposed to DAN (figure 4). These results suggest that while exposure to ALAN can increase reproductive output in all females, these impacts are strongest in smaller, younger lizards. These individuals are likely entering their first breeding season and are laying their first eggs earlier than they otherwise would. Because eggs produced early in the season have higher fitness in brown anoles [70], this phenological shift may be adaptive for mothers exposed to ALAN.

While early onset and increased frequency of egg production due to ALAN could result in smaller or otherwise lower quality eggs and hatchlings, we found only weak evidence that such a trade-off may exist in this system. For the set of first eggs produced by females, we found no differences in the size of mothers laying these eggs or the quality of the eggs themselves based on female exposure to ALAN, indicating that egg-laying induced by ALAN produces high-quality eggs. Eggs did not differ in mass or water content, but mothers exposed to ALAN did produce eggs with yolk content averaging 5.8% less than mothers in the DAN treatment. There was a non-significant trend towards lower hatching success of eggs from mothers exposed to ALAN, but exposure to ALAN did not affect hatchling size or quality. These results suggest that increased reproduction due to ALAN may come at some small costs to egg quality. However, given its strong positive impact on output and lack of effects on hatchling quality, it is likely that ALAN still has strong positive effects on reproductive output and fitness. Taken together, these effects appear particularly strong for

younger females which experience enhanced growth, earlier laying, and a doubling of reproductive output.

At least two aspects of our maintenance of anoles in the laboratory may have removed potential costs present in the field: energy availability and lack of predators. Anoles were fed at a standard rate generally considered to be *ad libitum* that assures a constant access to food. Under field conditions, prey is unlikely to be as continuously available to anoles as it was in the laboratory, though in some situations urban areas may have elevated abundances of arthropod prey [71]. The presence of ALAN in the laboratory may have increased appetite or could have allowed anoles to forage more consistently than their counterparts in the DAN treatment [38]. Indeed, many organisms, including reptiles, are known to expand nocturnal foraging in the presence of ALAN (the night-light niche; [21,22,72]) and may experience increased energy intake. An increase in foraging and energy intake in the ALAN treatment could have supported observed increases in growth and egg production of smaller females which may be more energy limited than larger females. We did not conduct nocturnal observations of anoles in our experiment to prevent additional stress to anoles in the ALAN treatment. However, many anole species have been observed foraging nocturnally under ALAN e.g. [18,45], including *A. sagrei* in the Miami area (C Thawley 2018, personal observation).

Anoles in the laboratory are also not exposed to the threat of predation. When ALAN is not present, anoles are strictly diurnal, and nocturnal activity may be dangerous for anoles [73,74]. Anoles in the field might restrict foraging under ALAN if predators are present, or anoles choosing to forage at ALAN sources may become prey themselves (e.g. [73]). As such, anoles in this study may have been able to forage nocturnally at rates they would not in the field or avoid normal costs of this activity. Additionally, this regime of ALAN coupled with high prey availability and predator absence occurred over a seven-week period. It is possible that costs could emerge were anoles exposed to these conditions on longer timescales, including across ontogeny.

Even given these considerations, it is still striking that brown anoles exposed to ALAN in the laboratory both increased growth and reproductive output compared to anoles in the DAN treatment. Earlier egg-laying allows for greater annual reproductive output which increases fitness. As an additional benefit, early season offspring have the highest fitness in *A. sagrei* [70], though this is not true for all organisms [26]. Likewise growth to larger body size has been linked to increased fitness in male and female anoles, where larger size can be related to greater intraspecific competitive ability, higher survival in the presence of predators, and higher reproductive output [57,59,75,76]. Thus, it appears that brown anoles may be able to make use of ALAN to increase fitness via multiple pathways.

Brown anoles are found in highly urbanized areas [42] where ALAN intensities are greatest, and they make use of ALAN for foraging in urban areas where they are invasive (e.g. [46,47]). While our work shows that this exploitation of ALAN could be adaptive in some contexts, it remains unclear whether this use of ALAN increases fitness in urban habitats. While reproduction in anoles is difficult to study in the field, future work should focus on experimental manipulations of ALAN under field conditions. Behavioural observations of anoles at ALAN sources could elucidate whether they may choose to use ALAN where available

[62], whether increased energy due to use of this novel foraging niche may be driving enhanced growth and reproduction [16], and whether predation by nocturnal predators may be an important factor. Additional work should address endocrine impacts of ALAN including changes in negative feedback of the hypothalamic–pituitary–adrenal (HPA) axis and whether exposure to ALAN in the field impacts melatonin production similarly to laboratory exposure [40]. Combining both laboratory and field manipulations of ALAN offers the most effective approach to assess effects on a variety of organismal systems while including ecologically realistic scenarios in research programmes [17].

Our current results suggest that, in some contexts, the presence of ALAN may increase fitness for species that can exploit novel resources ALAN makes available while avoiding potential costs. Intriguingly, the ability to exploit the night-light niche may support invasiveness in some reptiles [18,77]. Anoles themselves are a prolific group of invaders, especially in urban areas where they are known to adapt behaviourally and morphologically to novel conditions [78,79]. Melatonin production in *Anolis* lizards also appears to be more resistant to reduction by exposure to light than in many other vertebrates, with *A. sagrei* showing particularly high resistance [40]. Of the 20 species of anoles which are known to be introduced, 70% ($n=14$) have been observed using ALAN (C Thawley 2019, personal observation). In this context, and given their resistance to the physiological impacts of ALAN, anoles may be in a position to increase fitness via exploitation of the novel niche created by ALAN in urban environments.

As such, we suggest that while ALAN can induce negative effects in many taxa, ALAN may create an ecological opportunity for some species. Species adept at exploiting urban environments with ALAN may experience enhanced energy acquisition, growth, and reproduction, and, in turn, fitness [16]. The ability to tolerate or exploit ALAN may serve as a filter determining which species take advantage of or become invasive in urban environments. Our knowledge of how exposure to ALAN affects organisms remains taxonomically limited. Work that examines whether taxa show weak suppression of melatonin production when exposed to light may offer a novel avenue to predict which species are capable of invading environments with ALAN. We recommend that future studies test explicitly for both positive and negative impacts of ALAN, and consider the possibility of both plastic and evolutionary responses that may allow organisms to take advantage of the novel ecological space ALAN creates [11,80].

Ethics. All guidelines and procedures for the use of animals were approved by the Institutional Animal Care and Use Committee of University of Rhode Island (Protocol AN11-09-005)

Data accessibility. All data available from the Dryad digital Repository: <https://doi.org/10.5061/dryad.wpzgmsbgt> [81].

Authors' contributions. C.J.T. and J.J.K. conceived and designed the study and drafted the manuscript. C.J.T. carried out field and laboratory work and analysed data.

Competing interests. We declare we have no competing interests.

Funding. C.J.T. was funded by an NSF PRFB (grant no. 1711564), and this research was supported by NSF (grant no. DEB-1354897) to J.J.K.

Acknowledgements. We thank S. Michaelides, C. de Jesus Villanueva, A. Merritt, and Z. Chejanovski for assistance with anole maintenance and egg collection; D. Cardace for access to the drying oven; URI-INBRE for access to the plate reader and M. Patrick Griffith for access to catch lizards on plants at Montgomery Botanical Center.

- Acuto M, Parnell S, Seto KC. 2018 Building a global urban science. *Nat. Sustain.* **1**, 2–4. (doi:10.1038/s41893-017-0013-9)
- Jiang L, O'Neill BC. 2017 Global urbanization projections for the Shared Socioeconomic Pathways. *Glob. Environ. Change* **42**, 193–199. (doi:10.1016/j.gloenvcha.2015.03.008)
- Ditchkoff SS, Saalfeld ST, Gibson CJ. 2006 Animal behavior in urban ecosystems: modifications due to human-induced stress. *Urban Ecosyst.* **9**, 5–12. (doi:10.1007/s11252-006-3262-3)
- Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006 From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* **21**, 186–191. (doi:10.1016/j.tree.2005.11.019)
- Rizwan AM, Dennis LYC, Liu C. 2008 A review on the generation, determination and mitigation of Urban Heat Island. *J. Environ. Sci.* **20**, 120–128. (doi:10.1016/S1001-0742(08)60019-4)
- Forman RTT. 2014 *Urban ecology: science of cities*. Cambridge, UK: Cambridge University Press.
- Battles AC, Moniz M, Kolbe JJ. 2018 Living in the big city: preference for broad substrates results in niche expansion for urban *Anolis* lizards. *Urban Ecosyst.* **21**, 1087–1095. (doi:10.1007/s11252-018-0787-1)
- Gaston KJ, Duffy JP, Gaston S, Bennie J, Davies TW. 2014 Human alteration of natural light cycles: causes and ecological consequences. *Oecologia* **176**, 917–931. (doi:10.1007/s00442-014-3088-2)
- Kyba CCM *et al.* 2017 Artificially lit surface of Earth at night increasing in radiance and extent. *Sci. Adv.* **3**, e1701528. (doi:10.1126/sciadv.1701528)
- Horton KG, Nilsson C, Van Doren BM, La Sorte FA, Dokter AM, Farnsworth A. 2019 Bright lights in the big cities: migratory birds' exposure to artificial light. *Front. Ecol. Environ.* **17**, 209–214. (doi:10.1002/fee.2029)
- Hopkins GR, Gaston KJ, Visser ME, Elgar MA, Jones TM. 2018 Artificial light at night as a driver of evolution across urban–rural landscapes. *Front. Ecol. Environ.* **16**, 472–479. (doi:10.1002/fee.1828)
- Rich C, Longcore T. 2006 *Ecological consequences of artificial night lighting*, p. 458. Washington, DC: Island Press.
- Gaston KJ, Visser ME, Hölker F. 2015 The biological impacts of artificial light at night: the research challenge. *Phil. Trans. R. Soc. B* **370**, 20140133. (doi:10.1098/rstb.2014.0133)
- Navara KJ, Nelson RJ. 2007 The dark side of light at night: physiological, epidemiological, and ecological consequences. *J. Pineal Res.* **43**, 215–224. (doi:10.1111/j.1600-079X.2007.00473.x)
- Bedrosian TA, Fonken LK, Walton JC, Nelson RJ. 2011 Chronic exposure to dim light at night suppresses immune responses in Siberian hamsters. *Biol. Lett.* **7**, 468–471. (doi:10.1098/rsbl.2010.1108)
- Welbers AAMH, van Dis NE, Kolvoort AM, Ouyang J, Visser ME, Spoelstra K, Dominoni DM. 2017 Artificial light at night reduces daily energy expenditure in breeding great tits (*Parus major*). *Front. Ecol. Evol.* **5**, 55. (doi:10.3389/fevo.2017.00055)
- Ouyang JQ, Davies S, Dominoni D. 2018 Hormonally mediated effects of artificial light at night on behavior and fitness: linking endocrine mechanisms with function. *J. Exp. Biol.* **221**, jeb156893. (doi:10.1242/jeb.156893).
- Perry G, Buchanan BW, Fisher RN, Salmon M, Wise SE. 2008 Effects of artificial night lighting on amphibians and reptiles in urban environments. In *Urban herpetology* (eds JC Mitchell, RE Jung Brown, B Bartholomew), pp. 239–256. Salt Lake City, UT: Society for the Study of Amphibians and Reptiles.
- Rodríguez A *et al.* 2017 Seabird mortality induced by land-based artificial lights. *Conserv. Biol.* **31**, 986–1001. (doi:10.1111/cobi.12900)
- Dwyer RG, Bearhop S, Campbell HA, Bryant DM. 2013 Shedding light on light: benefits of anthropogenic illumination to a nocturnally foraging shorebird. *J. Anim. Ecol.* **82**, 478–485. (doi:10.1111/1365-2656.12012)
- Rydell J. 1992 Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* **6**, 744–750. (doi:10.2307/2389972)
- Willmott NJ, Henneken J, Elgar MA, Jones TM. 2019 Guiding lights: foraging responses of juvenile nocturnal orb-web spiders to the presence of artificial light at night. *Ethology* **125**, 289–297. (doi:10.1111/eth.12852)
- de Jong M, Ouyang JQ, Da Silva A, van Grunsven RHA, Kempenaers B, Visser ME, Spoelstra K. 2015 Effects of nocturnal illumination on life-history decisions and fitness in two wild songbird species. *Phil. Trans. R. Soc. B* **370**, 20140128. (doi:10.1098/rstb.2014.0128)
- Jones TM, Durrant J, Michaelides EB, Green MP. 2015 Melatonin: a possible link between the presence of artificial light at night and reductions in biological fitness. *Phil. Trans. R. Soc. B* **370**, 20140122. (doi:10.1098/rstb.2014.0122)
- Dominoni DM, Goymann W, Helm B, Partecke J. 2013 Urban-like night illumination reduces melatonin release in European blackbirds (*Turdus merula*): implications of city life for biological time-keeping of songbirds. *Front. Zool.* **10**, 1–11. (doi:10.1186/1742-9994-10-60)
- Lambrechts MM, Blondel J, Maistre M, Perret P. 1997 A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc. Natl. Acad. Sci. USA* **94**, 5153–5155. (doi:10.1073/pnas.94.10.5153)
- Kempenaers B, Borgström P, Loës P, Schlicht E, Valcu M. 2010 Artificial night lighting affects dawn song, extra-pair siring success, and lay date in songbirds. *Curr. Biol.* **20**, 1735–1739. (doi:10.1016/j.cub.2010.08.028)
- Dawson A, King VM, Bentley GE, Ball GF. 2001 Photoperiodic control of seasonality in birds. *J. Biol. Rhythms* **16**, 365–380. (doi:10.1177/074873001129002079)
- Botte V, Angelini F, Picariello O. 1978 Autumn photothermal regimes and spring reproduction in the female lizard, *Lacerta sicula*. *Herpetologica* **34**, 298–302.
- Licht P. 1971 Regulation of the annual testis cycle by photoperiod and temperature in the lizard *Anolis carolinensis*. *Ecology* **52**, 240–252. (doi:10.2307/1934582)
- Licht P. 1973 Influence of temperature and photoperiod on the annual ovarian cycle in the lizard *Anolis carolinensis*. *Copeia* **1973**, 465–472. (doi:10.2307/1443111)
- Salisbury FB. 1981 Responses to photoperiod. In *Physiological plant ecology I* (eds OL Lange, PS Nobel, CB Osmond, H Ziegler), pp. 135–167. Berlin, Germany: Springer.
- Cagnacci A, Volpe A. 1996 Influence of melatonin and photoperiod on animal and human reproduction. *J. Endocrinol. Invest.* **19**, 382–411. (doi:10.1007/bf03344974)
- Fenner M. 1998 The phenology of growth and reproduction in plants. *Perspect. Plant Ecol. Evol. Syst.* **1**, 78–91. (doi:10.1078/1433-8319-00053)
- Ouyang JQ, de Jong M, Hau M, Visser ME, van Grunsven RHA, Spoelstra K. 2015 Stressful colours: corticosterone concentrations in a free-living songbird vary with the spectral composition of experimental illumination. *Biol. Lett.* **11**, 8. (doi:10.1098/rsbl.2015.0517)
- Mitchell J, Jung R, Bartholomew B. 2008 *Urban herpetology*. Salt Lake City, UT: Society for the Study of Amphibians and Reptiles.
- French SS, Webb AC, Hudson SB, Virgin EE. 2018 Town and country reptiles: a review of reptilian responses to urbanization. *Integr. Comp. Biol.* **58**, 948–966. (doi:10.1093/icb/icy052)
- Fox W, Dessauer HC. 1957 Photoperiodic stimulation of appetite and growth in the male lizard, *Anolis carolinensis*. *J. Exp. Zool.* **134**, 557–575. (doi:10.1002/jez.1401340308)
- Mayer I, Bornestaf C, Borg B. 1997 Melatonin in non-mammalian vertebrates: physiological role in reproduction? *Comp. Biochem. Phys. A* **118**, 515–531. (doi:10.1016/S0300-9629(96)00468-9)
- Moore AF, Menaker M. 2011 The effect of light on melatonin secretion in the cultured pineal glands of *Anolis* lizards. *Comp. Biochem. Phys. A* **160**, 301–308. (doi:10.1016/j.cbpa.2011.06.027)
- Underwood H. 1986 Light at night cannot suppress pineal melatonin levels in the lizard *Anolis carolinensis*. *Comp. Biochem. Phys. A* **84**, 661–663. (doi:10.1016/0300-9629(86)90382-8)
- Kolbe JJ, VanMiddlesworth P, Battles AC, Stroud JT, Buffum B, Forman RTT, Losos JB. 2016 Determinants of spread in an urban landscape by an introduced lizard. *Landscape Ecol.* **31**, 1795–1813. (doi:10.1007/s10980-016-0362-1)
- Lee JC, Clayton D, Eisenstein S, Perez I. 1989 The reproductive cycle of *Anolis sagrei* in southern

- Florida. *Copeia* **1989**, 930–937. (doi:10.2307/1445979)
44. Norval G, Slater K, Brown LR, Mao J-J, Goldberg SR. 2019 Interrelation of fat body mass, liver mass, and environmental parameters on the reproductive cycle of the brown anole (*Anolis sagrei*), an introduced lizard in Taiwan. *Herpetol. Conserv. Biol.* **14**, 67–79.
 45. Maurer AS, Thawley CJ, Fireman AL, Giery ST, Stroud JT. 2019 Nocturnal activity of Antiguan lizards under artificial light. *Herpetol. Conserv. Biol.* **14**, 105–110.
 46. Meshaka J, Walter E, Butterfield BP, Hauge JB. 2004 *The exotic amphibians and reptiles of Florida*, p. 166. Malabar, FL: Krieger Publishing Company.
 47. Brown TW, Arrivillaga C. 2017 Nocturnal activity facilitated by artificial lighting in the diurnal *Norops sagrei* (Squamata: Dactyloidae) on Isla de Flores, Guatemala. *Mesoam. Herpetol.* **4**, 637–639.
 48. Warner DA, Johnson MS, Nagy TR. 2016 Validation of body condition indices and quantitative magnetic resonance in estimating body composition in a small lizard. *J. Exp. Zool. A* **325**, 588–597. (doi:10.1002/jez.2053)
 49. Romero LM, Reed JM. 2005 Collecting baseline corticosterone samples in the field: is under 3 min good enough? *Comp. Biochem. Phys. A* **140**, 73–79. (doi:10.1016/j.cbpb.2004.11.004)
 50. Tylan C et al. 2020 Obtaining plasma to measure baseline glucocorticoid concentrations in reptiles: How quick is quick enough? *Gen. Comp. Endocr.* (doi:10.1016/j.ygcen.2019.113324)
 51. Lenth R. 2018 emmeans: estimated marginal means, aka least-squares means. v 1.2.2.
 52. Therneau TM. 2015 A package for survival analysis in S. v 2.38.
 53. Jackson C. 2016 flexsurv: a platform for parametric survival modeling in R. *J. Stat. Softw.* **70**, 33. (doi:10.18637/jss.v070.i08)
 54. Bates D, Maechler M, Bolker B, Walker S. 2015 Fitting linear mixed effect models using lme4. *J. Stat. Soft.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
 55. R Core Team. 2018 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
 56. Ouyang JQ, de Jong M, van Grunsven RHA, Matson KD, Haussmann MF, Meerlo P, Visser ME, Spoelstra K. 2017 Restless roosts: light pollution affects behavior, sleep, and physiology in a free-living songbird. *Glob. Change Biol.* **23**, 4987–4994. (doi:10.1111/gcb.13756)
 57. Tokarz RR. 1985 Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.* **33**, 746–753. (doi:10.1016/S0003-3472(85)80006-3)
 58. Kolbe JJ, Ehrenberger JC, Moniz HA, Angilletta Jr. MJ. 2014 Physiological variation among invasive populations of the brown anole (*Anolis sagrei*). *Physiol. Biochem. Zool.* **87**, 92–104. (doi:10.1086/672157)
 59. Warner DA, Buckelew AM, Pearson PR, Dhawan A. 2015 The effect of prey availability on offspring survival depends on maternal food resources. *Biol. J. Linn. Soc.* **2015**, 437–447. (doi:10.1111/bij.12519)
 60. Kitaysky AS, Piatt JF, Hatch SA, Kitaiskaia EV, Benowitz-Fredericks ZM, Shultz MT, Wingfield JC. 2010 Food availability and population processes: severity of nutritional stress during reproduction predicts survival of long-lived seabirds. *Funct. Ecol.* **24**, 625–637. (doi:10.1111/j.1365-2435.2009.01679.x)
 61. Durrant J, Green MP, Jones TM. 2019 Dim artificial light at night reduces the cellular immune response of the black field cricket, *Teleogryllus commodus*. *Insect Sci.* (doi:10.1111/1744-7917.12665)
 62. Ulgezen ZN, K pyl  T, Meerlo P, Spoelstra K, Visser ME, Dominoni DM. 2019 The preference and costs of sleeping under light at night in forest and urban great tits. *Proc. R. Soc. B* **286**, 20190872. (doi:10.1098/rspb.2019.0872)
 63. Fleischer Jr AL, Bowman R, Woolfenden GE. 2003 Variation in foraging behavior, diet, and time of breeding of Florida Scrub-Jays in suburban and wildland habitats. *Condor Ornithol. Appl.* **105**, 515–527. (doi:10.1650/7224)
 64. Licht P, Gorman GC. 1970 *Reproductive and fat cycles in Caribbean anolis lizards*, vol. 95, pp. 1–52. University of California Publications in Zoology. Berkeley, CA: University of California Press.
 65. Gorman GC, Licht P. 1974 Seasonality in ovarian cycles among tropical *Anolis* lizards. *Ecology* **55**, 360–369. (doi:10.2307/1935223)
 66. Fox W, Dessauer HC. 1958 Response of the male reproductive system of lizards (*Anolis carolinensis*) to unnatural day-lengths in different seasons. *Biol. Bull.* **115**, 421–439. (doi:10.2307/1539107)
 67. Levey IL. 1973 Effects of pinealectomy and melatonin injections at different seasons on ovarian activity in the lizard *Anolis carolinensis*. *J. Exp. Zool.* **185**, 169–174. (doi:10.1002/jez.1401850205)
 68. Mayhew WW. 1961 Photoperiodic response of female fringe-toed lizards. *Science* **134**, 2104–2105. (doi:10.1126/science.134.3496.2104)
 69. Mayhew WW. 1964 Photoperiodic responses in three species of the lizard genus *Uma*. *Herpetologica* **20**, 95–113.
 70. Pearson PR, Warner DA. 2018 Early hatching enhances survival despite beneficial phenotypic effects of late-season developmental environments. *Proc. R. Soc. B* **285**, 20180256. (doi:10.1098/rspb.2018.0256)
 71. Cook WM, Faeth SH. 2006 Irrigation and land use drive ground arthropod community patterns in an urban desert. *Environ. Entomol.* **35**, 1532–1540. (doi:10.1093/ee/35.6.1532)
 72. Garber SD. 1978 Opportunistic feeding behavior of *Anolis cristatellus* (Iguanidae: Reptilia) in Puerto Rico. *Trans. Kans. Acad. Sci.* **81**, 79–80. (doi:10.2307/3627360)
 73. Perry G, Lazell J. 2000 Natural history: *Liophis portoricensis anegadae* (Puerto Rican racer), Night-light niche. *Herpetol. Rev.* **31**, 247.
 74. Perry G, Fisher RN. 2006 Night lights and reptiles: observed and potential effects. In *Ecological consequences of artificial night lighting* (eds C Rich, T Longcore), pp. 169–191. Washington, DC: Island Press.
 75. Losos JB, Schoener TW, Spiller DA. 2004 Predator-induced behaviour shifts and natural selection in field-experimental lizard populations. *Nature* **432**, 505–508. (doi:10.1038/nature03039)
 76. Chejanovski ZA, Kolbe JJ. 2019 Close encounters of the urban kind: predators influence body size variation in an urban landscape. *Evol. Ecol.* **33**, 791–809. (doi:10.1007/s10682-019-10008-1)
 77. Zozaya SM, Alford RA, Schwarzkopf L. 2015 Invasive house geckos are more willing to use artificial lights than are native geckos. *Aust. Ecol.* **40**, 982–987. (doi:10.1111/aec.12287)
 78. Lapiedra O, Chejanovski Z, Kolbe JJ. 2017 Urbanization and biological invasion shape animal personalities. *Glob. Change Biol.* **23**, 592–603. (doi:10.1111/gcb.13395)
 79. Winchell KM, Maayan I, Fredette JR, Revell LJ. 2018 Linking locomotor performance to morphological shifts in urban lizards. *Proc. R. Soc. B* **285**, 1880. (doi:10.1098/rspb.2018.0229)
 80. Dominoni D, Quetting M, Partecke J. 2013 Artificial light at night advances avian reproductive physiology. *Proc. R. Soc. B* **280**, 9. (doi:10.1098/rspb.2012.3017)
 81. Thawley CJ, Kolbe JJ. 2020 Data from: Artificial light at night increases growth and reproductive output in *Anolis* lizards. Dryad Digital Repository. (<https://doi.org/10.5061/dryad.wpzgmsbgt>)