

## RESEARCH ARTICLE

# Sleeping Under Pressure: Sleep Site Selection in Urban Brown Anole Lizards (*Anolis sagrei*)

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## ABSTRACT

Daytime microhabitat selection is shaped by both physiological traits and environmental pressures, yet nocturnal microhabitat selection remains poorly understood in many species. In urban brown anole lizards (*Anolis sagrei*), daytime perch selection is influenced by morphology, thermoregulation, and competition, but the factors shaping nocturnal perch selection in urban populations are less clear. We examined sleep site selection at night in adult male, adult female, and juvenile brown anoles in an urban population in New Orleans, Louisiana. Larger individuals perched marginally higher than smaller conspecifics, though perch height did not differ significantly across groups. Within juveniles, higher body temperatures were associated with lower perch heights, a pattern not observed in adults. This difference may reflect active thermoregulatory behavior on the part of juveniles, or passive heat gain resulting from lower thermal inertia. Most lizards slept facing the stem of the plant, suggesting a defensive posture toward potential ground-based predators. Individuals also slept in dark sleeping perches, with most observed at light levels below 1lx, microhabitats that may reduce predator detection or exposure to artificial light at night (ALAN). Overall, sleep site selection in this urban population of *A. sagrei* exhibits marked variation within the studied population, and likely reflects the combined influence of morphology, light exposure, predation risk, and age-specific constraints.

## 1 | Introduction

Animals distribute themselves within available habitats based on a variety of extrinsic and intrinsic factors (Huey 1991). These decisions are ultimately shaped by natural selection, such that many species exhibit specific habitat preferences rather than passively tracking habitat availability (Johnson 1980). These choices affect survival and reproduction by influencing exposure to predators, access to resources, and environmental stress. Although many studies focus on habitat use during active periods, far less is known about how animals choose sleep sites, despite these periods also representing times of heightened vulnerability (Lima et al. 2005). Sleep sites can influence energy balance and circadian regulation, and are often selected to minimize danger while meeting physiological demands (Eban-Rothschild et al. 2017; Helfrich-Förster 2017; Aulsebrook

et al. 2016). Across diverse taxa, sleep site selection reflects species-specific solutions to ecological pressures. For example, wolverines (*Gulo gulo*) exhibit context-dependent trade-offs by choosing between subnivean cavities and surface snow beds depending on temperature and predation risk (Glass et al. 2021), whereas proboscis monkeys (*Nasalis larvatus*) prefer riverside trees that reduce mosquito exposure and predator access (Feilen and Marshall 2014). In birds, sleep site selection is shaped by predation risk, temperature, and light conditions. Artificial light at night (ALAN) specifically can reduce sleep duration and quality, with downstream effects on performance and cognition (Aulsebrook et al. 2020, 2021; Spoelstra and Visser 2014).

There is also a growing literature highlighting urbanization's effects on sleep behavior in various taxa due to the common and replicated differences between urban and undisturbed

environments (reviewed in Raap et al. 2015; Mohanty, Wagener, et al. 2021). ALAN, fragmented vegetation, and altered thermal environments can drive parallel adaptations across cities, as demonstrated by shifts in thermal tolerance (Campbell-Staton et al. 2020) and morphology or locomotor performance in some urban lizards (Winchell et al. 2018). However, the consequences of urbanization for sleep site selection, particularly for intraspecific variation, remain poorly understood. This gap is particularly notable given both the global scale of urban expansion and the potential fitness consequences of poor sleep site choice for an increasing number of species. Understanding the factors driving variation in sleep site selection and general nighttime ecology in urban environments should therefore be a priority.

Lizards of the genus *Anolis* are an ideal system for studying habitat use, including sleep site selection, because of their abundance, ecological diversity, and well-documented morphological variation (Losos 2009). Caribbean anoles display ecomorphs that specialize in structural microhabitats (Williams 1983), and their daytime perch use varies predictably with body size, locomotor traits, and social context (Irschick and Losos 1999; Losos et al. 1993). Such well-characterized ecological and morphological differences make *Anolis* a powerful model for testing how animals determine nocturnal perch use. Existing research suggests that some anoles often sleep on higher, narrower, and more horizontal perches than those used during the day, likely to reduce detection or facilitate escape from nocturnal predators (Singhal et al. 2007; Poche et al. 2005; Mohanty, Joshi, and Thaker 2021). In two Puerto Rican anole species, larger individuals (> 50 mm) sleep higher (Clark and Gillingham 1990), possibly to avoid ground-based predators, although such sites may also increase visibility to aerial predators. Sleep positioning may also play a role in predator avoidance such that many lizards sleep with their snouts oriented toward the perch stem, likely enhancing their ability to detect and escape from threats (Clark and Gillingham 1990; Bors et al. 2022; Cabrera-Guzmán and Reynoso 2010). Despite these general insights, relatively few studies have considered sleep site selection and nocturnal habitat use in urban *Anolis* populations.

The brown anole, *Anolis sagrei*, is a small, diurnal lizard native to Cuba and the Bahamas that has successfully invaded large portions of the southeastern United States. It is particularly abundant in cities, where its behavioral flexibility and high population density make it well suited for field studies of urban ecology (Losos et al. 1993; Kolbe et al. 2004; Fetters and McGlothlin 2017). Daytime perch height in *A. sagrei* differs by sex and age class, with adult males typically occupying the highest perches (Delaney and Warner 2016), but it remains unclear whether these patterns persist at night under different constraints. Additionally, juvenile *A. sagrei* may differ from adults in thermal preferences or sensitivity due to their small body size and rapid heat exchange (Walguarnery et al. 2012), which could lead to differences in perch use. Recent experimental work in Miami, Florida found that *A. sagrei* did not alter their sleep site selection in response to ALAN. Despite being exposed to elevated light levels, individuals remained in illuminated sleep sites rather than relocating to safer or darker microhabitats. As a result, they exhibited increased nighttime responsiveness and reduced daytime performance

(Kolbe et al. 2021). However, the factors affecting intraspecific variation in sleep site selection in unmanipulated populations in response to variation in ecological pressures, such as ALAN remain poorly understood.

In this study, we investigated sleep site selection in an urban population of *A. sagrei* in New Orleans, Louisiana. We hypothesized that individuals select sleep sites non-randomly based on perch characteristics, environmental conditions, and intraspecific differences. Specifically, we predicted that larger individuals would sleep on higher perches than smaller ones, reflecting differences in predation risk with body size or competitive ability. In addition, we expected adult males to sleep higher than females and juveniles, consistent with their greater size and territoriality. We predicted that lizards would orient their snouts toward the perch stem to enhance predator detection and facilitate escape. Finally, we predicted individuals would prefer darker perches and avoid brighter areas due to potential sleep disruption from ALAN.

## 2 | Methods

### 2.1 | Site Description

Brown anoles (*Anolis sagrei*,  $N=93$ ) were sampled at Walter "Wolfman" Washington Memorial Park ( $29.98005^{\circ}$  N,  $-90.08454^{\circ}$  W), located in an urban area of New Orleans, Louisiana. The park covers a triangular area of approximately 1600 square meters and is bordered on all three sides by streets, with adjacent residential buildings and commercial establishments. The park contains paved sidewalks, open lawn, and diverse vegetation suitable for perching, similar to other urban sites in New Orleans where *Anolis* habitat use has been studied (e.g., Irschick, Carlisle, et al. 2005; Irschick et al. 2006; Edwards and Lailvaux 2012; Weber et al. 2021). Surveys were conducted in vegetated areas containing shrubs, trees, ground cover, vines, palms, and cycads, which were systematically sampled.

### 2.2 | Random Habitat Sampling Measurements

We conducted random habitat sampling at the study site before capturing lizards for morphological measurements. Following the methods of Irschick, Vanhooydonck, et al. (2005) and Edwards and Lailvaux (2012), we placed a custom-built quadrat measuring 2 m in height and 1.5 m in width, with horizontal twine attached at heights of 0.5, 1, and 2 m, to systematically assess available perches. Random habitat sampling points were spaced at approximately 10 m intervals throughout Walter "Wolfman" Washington Memorial Park to ensure broad coverage of the habitat. At each quadrat location, we recorded the length, height, and width of all potential perches within 5 cm of the quadrat. A structure was considered a potential perch if it appeared physically capable of supporting the weight of *A. sagrei*, based on general knowledge of the species' size and perching behavior and following the methods of Irschick, Vanhooydonck, et al. (2005) and Edwards and Lailvaux (2012). Measurements were taken using a measuring tape for length, height, and width. We excluded artificial structures, such as fences, walls, and benches. A total of 151 potential perches were recorded

at 13 locations throughout Walter “Wolfman” Washington Memorial Park.

### 2.3 | Sleep Perch Surveys

Lizard sleep perch surveys took place on 22 nights in Walter “Wolfman” Washington Memorial Park from July 1 to August 31, 2024, from 09:00 p.m. to 11:30 p.m. This timeframe was selected based on preliminary observations of typical periods of nocturnal rest for *A. sagrei* with the aim of ensuring that measurements were made during periods when the majority of individuals in the population are asleep. A total of 93 individuals were recorded. Of these, 24 were adult males, 23 were adult females, and 46 were juveniles. Each survey involved thoroughly scanning all potential perches in the study area, ensuring that we did not bias our dataset by focusing only on locations where lizards were more likely to be found during the day. Sleeping lizards were identified based on specific behavioral indicators: their eyes were closed, their bodies exhibited a prone posture against the substrate, and one or both hind limbs were typically extended (Libourel et al. 2018; Albeck et al. 2022). In this state, all typical antipredator behaviors (i.e., escape responses and defensive posturing) were absent unless the lizard was disturbed. When a sleeping lizard was located, a photograph was taken of the lizard on its perch. The lizard was then carefully hand-captured, and we measured cloacal temperature using a thermocouple (Omega HH806AU). Afterward, we weighed the lizard using a portable scale, and used digital calipers (Mitutoyo 6 “Digimatic Caliper, Model CD-6” CX, 500-171-20) to measure snout–vent length (SVL); head width; head length; head depth; humerus length; radius length; longest front toe; femur length; tibia length; longest back toe; and tail length. Lizards were marked with a black mark below the cloaca in case of later recapture to limit recording details of an individual more than once (following Lailvaux 2020; Husak and Lailvaux 2019; Irschick, Carlisle, et al. 2005).

We measured perch height, width, and length using a tape measure. Perch width was measured as the horizontal diameter of the structure on which the lizard was sleeping. Perch length was measured from the proximal base to the distal tip of the structure supporting the lizard, such as a leaf blade or any surface between two nodes (Irschick, Vanhooydonck, et al. 2005; Edwards

and Lailvaux 2012). Lizards were returned to their perches immediately after measurements.

Sleeping orientation was classified based on the snout's direction relative to the root of the perch. Following conventions in the literature (Clark and Gillingham 1990; Cabrera-Guzmán and Reynoso 2010; Mohanty et al. 2016), orientations were categorized as “toward” (snout facing the perch base or stem), “away” (snout facing the tip or distal end of the perch), or “perpendicular” (snout aligned laterally to the perch axis).

Light intensity at the perch was quantified using a BTMETER BT-881D digital lux meter (Table 1). Due to logistical and methodological constraints, we did not measure lux levels at randomly sampled habitat perches. Specifically, accurately assessing lux at night is sensitive to subtle changes in angle and shadowing which vary across the park environment. In contrast to structural perch characteristics (e.g., length and width), which remain stable across day and night, lux values fluctuate with artificial lighting sources. As a result, we restricted lux measurements to sleep perches where lizards were located. All procedures were approved by the University of New Orleans IACUC #24-011.

### 2.4 | Statistical Analyses

All statistical analyses were conducted in R 4.3.1 (R Core Team 2023). To meet the assumptions of parametric tests, we assessed the normality of lizard morphology and perch characteristic data using Shapiro–Wilk tests and applied Box–Cox transformations to all variables to ensure consistency for principal component analysis (PCA) and parametric tests. Transformed data were used for PCA and Welch's *t*-tests; untransformed data were used for non-parametric tests. To test the hypothesis that sleeping perches differ from randomly available habitat, we used Kolmogorov–Smirnov tests to compare perch characteristics (height, width, and length) between actual sleep sites and random samples. A MANOVA was conducted to assess whether perch height, perch width, and perch length differed by sex and age class. When the MANOVA indicated a significant multivariate effect, we followed up with univariate ANOVAs for each response variable.

To examine whether larger individuals select higher perches, we performed a PCA on Box–Cox transformed morphological traits

**TABLE 1** | Summary of perch characteristics, light intensity, and snout orientation for sleeping Adult Female, Adult Male, and Juvenile *A. sagrei* in Walter “Wolfman” Washington Memorial Park (Mean  $\pm$  SD for continuous variables; counts for position).

Perch characteristics	Adult female ( <i>n</i> = 23)	Adult male ( <i>n</i> = 24)	Juvenile ( <i>n</i> = 46)
Perch height	0.61 $\pm$ 0.28	0.72 $\pm$ 0.28	0.61 $\pm$ 0.30
Perch width	96.22 $\pm$ 163.03	75.87 $\pm$ 88.67	20.42 $\pm$ 26.15
Perch length	0.35 $\pm$ 0.30	0.54 $\pm$ 0.24	0.21 $\pm$ 0.20
Lux	0.56 $\pm$ 0.95	0.35 $\pm$ 0.65	0.33 $\pm$ 0.44
<b>Snout orientation</b>			
Toward	17	11	29
Away	4	11	12
Perpendicular	2	1	5

(body mass, SVL, head dimensions, limb lengths, tail length, and toe lengths) to derive a composite size variable. We then used PC1 scores in a linear regression with transformed perch height as the dependent variable. We also fit separate linear models for juveniles and adults with perch height as the dependent variable and body temperature as the predictor to examine potential age-specific differences in the relationship between microhabitat and thermal exposure or thermoregulation.

To determine whether individuals preferentially orient their snouts toward perch stems, we used a chi-squared test assuming an equal distribution of orientations. To test whether sleep orientation differed across sex and age classes, we used a Fisher's exact test.

To assess whether lizards disproportionately occupied darker sleep sites, we analyzed the distribution of lux values at sleep perches. We tested whether the median was lower than the midpoint of the observed range using a one-tailed Wilcoxon signed-rank test. To assess intraspecific variation, we used a Kruskal-Wallis rank sum test comparing lux values across age/sex categories (juvenile, adult male, and adult female).

### 3 | Results

*Anolis sagrei* in Walter "Wolfman" Washington Memorial Park was observed sleeping on a range of ornamental shrubs and plants. These included upright-growing species with long-bladed foliage, large-leaved tropicals, slender herbaceous or woody vines, and dense, multi-stemmed shrubs with small leaves. Lizards typically perched on elevated, exposed substrates extended away from the central part of the plant, either along the length of a leaf blade or on a narrow stem.

#### 3.1 | Sleep Sites vs. Available Habitat

A Kolmogorov-Smirnov test revealed significant differences between sleep sites and randomly sampled habitat perches in perch height ( $D=0.342$ ,  $p<0.001$ ), perch width ( $D=0.429$ ,  $p<0.001$ ), and perch length ( $D=0.308$ ,  $p<0.001$ ). Follow-up one-sided tests indicated that lizards tended to occupy lower perches ( $D^-=0.342$ ,  $p<0.001$ ), shorter perches ( $D^-=0.180$ ,  $p=0.024$ ), and wider perches ( $D^+=0.429$ ,  $p<0.001$ ) compared with random habitat.

#### 3.2 | Intraspecific Variation in Perch Use

A MANOVA revealed significant variation in perch characteristics by age and sex class (Pillai's Trace = 0.175,  $F=2.846$ ,  $p=0.011$ ). Although perch height did not vary significantly across groups ( $p=0.386$ ), significant differences were detected in perch width ( $p=0.033$ ) and perch length ( $p=0.011$ ) (Table 1).

#### 3.3 | Body Size and Perch Height

A PCA conducted on transformed morphological traits showed that the first two components explained 87.62% of total variance. PC1 (82.28%) was strongly associated with body size traits

(mass, SVL, and limb lengths), whereas PC2 (5.35%) reflected toe length variation. A linear regression revealed a significant but weak positive relationship between PC1 and transformed perch height ( $\beta=0.003$ ,  $R^2=0.048$ ,  $p=0.036$ ), indicating that individuals with larger overall body size tended to sleep slightly higher than smaller individuals (Figure 1).

#### 3.4 | Perch Height and Body Temperature

A linear regression revealed a significant negative relationship between body temperature and perch height among juveniles ( $\beta=-0.0095$ ,  $p=0.003$ ), with individuals selecting lower perches at warmer temperatures. The model explained 17.0% of the variation in perch height (Adjusted  $R^2=0.170$ ). No such relationship was observed among adults ( $\beta=0.0005$ ,  $p=0.878$ ) (Figure 3).

#### 3.5 | Snout Orientation at Sleep Sites

Across all individuals, the majority (61.3%) slept with their snouts facing toward the perch stem, whereas 30.1% faced away, and 8.6% were perpendicular. A chi-squared test found a significant deviation from a uniform distribution across categories ( $\chi^2(2)=39.16$ ,  $p<0.001$ ), indicating a population-level orientation preference (Figure 2). Within adult males specifically, the number of individuals facing toward and away from the perch stem was equal ( $n=11$  each; Table 1). A Fisher's exact test found no significant differences in orientation across age or sex classes ( $p=0.222$ ).

#### 3.6 | Light Intensity at Sleep Sites

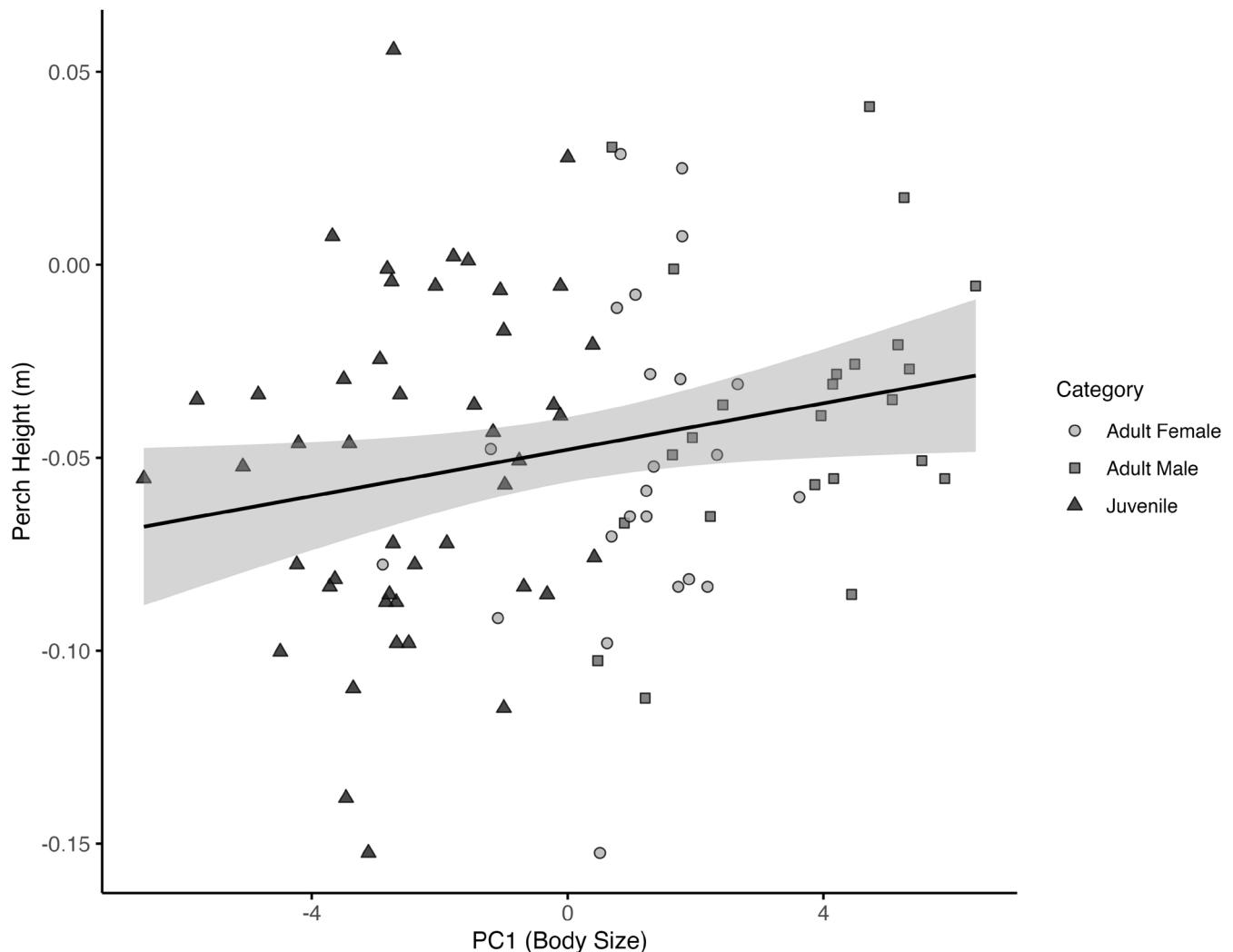
A Wilcoxon signed-rank test showed that the observed median lux value of selected sleep perches (0.151x) was significantly lower than the midpoint of the observed range (1.6851x;  $p<0.001$ ), indicating that most individuals occupied relatively dark sleep sites (Figure 4). This pattern did not differ significantly across age or sex classes, as a Kruskal-Wallis test revealed no differences in lux values among juveniles, adult males, and adult females ( $\chi^2=0.678$ ,  $df=2$ ,  $p=0.713$ ).

### 4 | Discussion

Sleep site selection can be affected by a variety of potential factors, ranging from habitat availability, predation risk, and environmental variation, to size, age, and sex. We tested the hypothesis that individuals within an urban population of brown anoles exhibit specific sleep site selection preferences based upon both environmental conditions and intraspecific variation in morphology and behavior.

Significant differences in perch height, width, and length between measured sleep sites and randomly available habitat indicate that *A. sagrei* actively selects perches with specific structural characteristics rather than occupying sites at random. Our random habitat sampling included vegetation up to 2 m tall, yet our results show that *A. sagrei* selected lower perches. This

## Relationship between Perch Height and PC1 in Sleeping *Anolis sagrei*



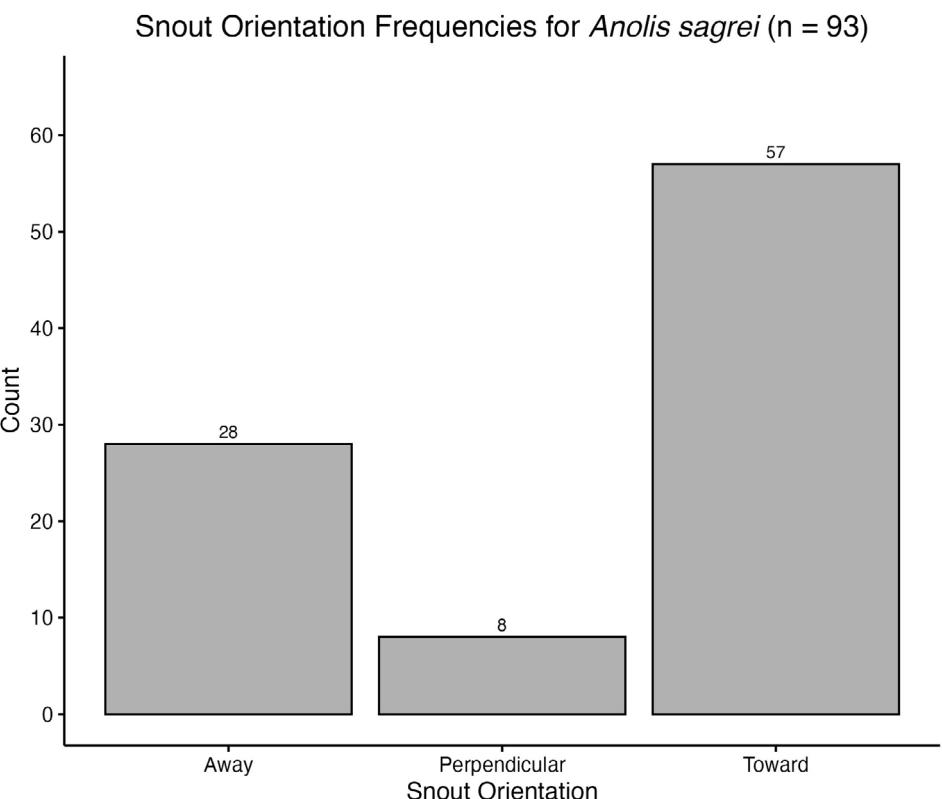
**FIGURE 1** | Relationship between perch height and body size (PC1) in sleeping *A. sagrei*. The scatterplot illustrates the positive association between body size (PC1 from PCA; negative values indicate smaller individuals, positive values larger individuals) and perch height (Box-Cox transformed; negative values represent transformed rather than absolute heights). Each point represents an individual lizard, color-coded by category (Adult Male, Adult Female, Juvenile). The solid black line shows the fitted linear regression, with a 95% confidence interval shaded in gray.

pattern aligns with the known ecology of *A. sagrei*, a trunk-ground ecomorph (Edwards and Lailvaux 2012).

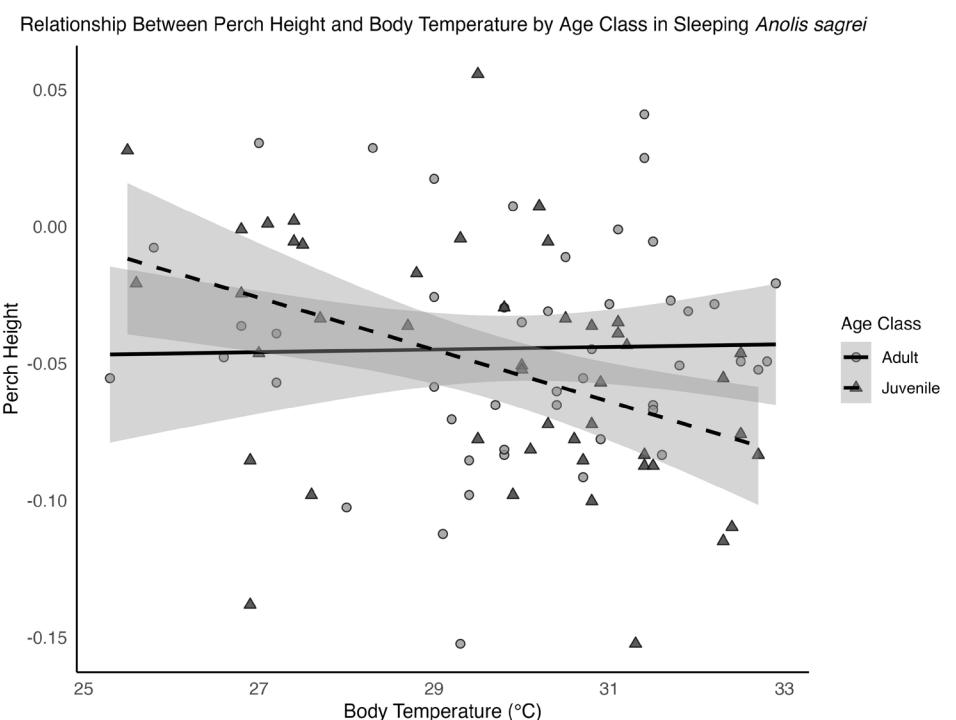
Our analyses revealed age- and sex-based differences in perch width and length. These structural features may reflect trade-offs in stability, accessibility, or predator detection across groups. Although body size was significantly associated with perch height, the relationship was weak ( $R^2=0.048$ ), suggesting that size alone explains little of the variation in nocturnal perch selection. This contrasts with expectations based on sexual dimorphism and growth-related size differences, which might predict a vertical stratification pattern (males > females > juveniles), as seen during the day (Delaney and Warner 2016). However, we found no significant group-level differences in perch height, suggesting that although larger lizards tend to sleep higher, perch height choices overlap broadly across size classes. This overlap implies dominance hierarchies or ontogenetic constraints play a limited role in shaping vertical sleep site selection. Instead, vertical sleep site selection may reflect shared ecological pressures,

such as predator avoidance, substrate availability, or microclimatic conditions. Higher sleep sites may reduce exposure to terrestrial predators and provide earlier access to basking opportunities at dawn (Mohanty, Wagener, et al. 2021), though this may come at the cost of increased visibility to nocturnal aerial predators like owls. The immobility of sleeping lizards may help mitigate this risk by reducing detection from visually oriented predators. Similar risk-balancing behavior has been documented in spiny-tailed iguanas (*Ctenosaura hemilopha*), which select elevated basking perches with nearby refuges to mitigate predation risk during long exposure periods (Blízquez and Rodríguez-Estrella 1997). The parallels in structural habitat use and predation avoidance underscore the importance of considering within-population morphological variation when interpreting habitat selection during vulnerable states like sleep.

Our data show that juvenile perch height was significantly associated with temperature: warmer individuals perched lower (Figure 3). Given their higher surface-area-to-volume ratio,



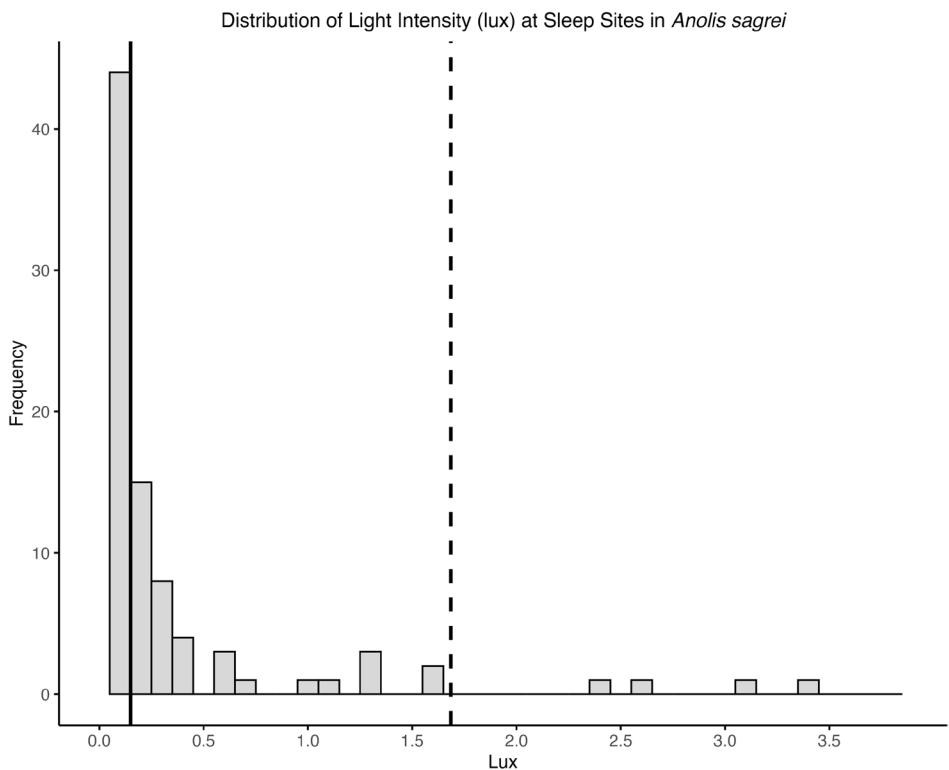
**FIGURE 2** | Snout orientation of sleeping *A. sagrei*. Toward (57), Away (28), and Perpendicular (8).



**FIGURE 3** | Relationship between perch height and body temperature by age class for sleeping *A. sagrei*. The scatterplot shows Box-Cox transformed perch height as a function of body temperature (°C), with points colored by age class: Pink = Adults (n = 47), blue = Juveniles (n = 46). Linear regressions with 95% confidence intervals are shown for each group. Perch height was significantly negatively associated with body temperature in juveniles ( $\beta = -0.0095, p = 0.003$ ), but not in adults ( $\beta = -0.0005, p = 0.878$ ).

juvenile anoles experience more rapid heat exchange than adults (Walguarnery et al. 2012). Therefore, juveniles may face stronger thermoregulatory pressures while asleep, or alternatively,

their elevated body temperatures may simply reflect the warmer microclimates of lower perches. Although anoles are often considered thermoconformers, Huey (1974) emphasized that



**FIGURE 4** | Distribution of light intensity (lux) for sleeping *A. sagrei*. The histogram shows the frequency of lux values recorded at sleep sites. The red solid line indicates the observed median lux across all sites (0.15lx), whereas the black dashed line marks the midpoint of the observed range (1.685lx).

thermoregulatory strategies are context-dependent, with individuals regulating or conforming based on ecological context and energetic cost. In this case, juveniles may select lower, warmer microhabitats overnight as an energetically favorable strategy to retain heat. In controlled daytime gradients, juvenile *A. sagrei* selected temperature ranges distinct from those preferred by juvenile *A. carolinensis*, and notably, these patterns ran opposite to those observed in adults (Walguarnery et al. 2012). This ontogenetic reversal where the direction of temperature preference shifts across life stages suggests that thermal habitat use is not fixed developmentally and supports the idea that juveniles may engage in behavioral thermoregulation even at night. Whether they are actively selecting warmer low perches or passively conforming to microclimate remains unclear, but future studies incorporating nighttime temperature manipulations could distinguish between physiological constraint and adaptive choice. Such work could also assess whether thermal sleep site selection influences juvenile performance or survival. Taken together, these results suggest that although many aspects of sleep behavior are conserved, thermal physiology and life stage may interact to shape nocturnal habitat use.

In addition to structural features like perch height, sleep site selection also reflected consistent behavioral patterns, particularly orientation relative to the perch stem. *Anolis sagrei* in our study population predominantly oriented their snouts toward the perch stem, deviating significantly from a random distribution (Figure 2). Raw counts showed that females and juveniles most often faced toward the stem, whereas adult males were evenly split between facing toward and away (Table 1). This positioning likely facilitates early predator detection and rapid

escape, as observed in other *Anolis* species (Cabrera-Guzmán and Reynoso 2010; Clark and Gillingham 1990) and distantly related taxa, such as *Monilesaurus rouxii*, *Coryphophylax subcristatus*, and *Coryphophylax brevicaudus* (Bors et al. 2022; Mohanty et al. 2016). The recurrence of this behavior across species suggests that sleep orientation may serve as a widespread antipredator strategy.

In contrast to Kolbe et al. (2021), who experimentally manipulated ALAN and found no substantial effect on sleep site selection in *A. sagrei* populations in Miami, our observational data from an urban New Orleans population suggest that individuals tend to occupy darker perches, with few observed sleeping in higher-lux microhabitats. This pattern was consistent across sex and age classes. Lux values at selected sleep sites ranged from 0.02 to 3.37lx, with most individuals (88%) occupying perches below 1lx (Figure 4), suggesting that brighter microhabitats were available but rarely used. These values approximate natural moonlight levels (0.05–2.10lx; Weaver 2011), such that *A. sagrei* may retain a behavioral tendency to occupy the darker portion of the urban light environment. Differences between our observational findings here and the experimental findings of Kolbe et al. (2021) may stem from ecological variation between urban settings. Miami harbors a greater diversity of reptile species, including several nocturnal and arboreal lizards, which could alter perceived risk or competitive pressures through niche partitioning and interspecific interactions (Clements et al. 2019). In contrast, the relatively low diversity at Walter “Wolfman” Washington Memorial Park in New Orleans may permit stronger expression of ALAN avoidance behaviors. Only two green anoles (*A. carolinensis*) were observed during

nocturnal surveys within our survey area, suggesting minimal overlap and reduced potential for interspecific competition at sleep sites. However, as we did not measure lux at unused perches, we cannot directly test for active selection against light. We interpret this consistent skew toward low lux values as ecologically meaningful, while acknowledging the methodological limitation. Comparative studies across urban gradients varying in light pollution, community composition, and predator abundance are needed to clarify the contexts in which ALAN shapes sleep site selection in lizards.

This study was conducted at a single, small urban site; therefore, observed patterns of sleep site selection may partly reflect local habitat constraints rather than general behavioral tendencies across populations. By examining fine-scale patterns within a single urban population, we demonstrate that although many aspects of sleep site selection are conserved across sex and age classes, variation emerges in relation to body size and thermal context. This suggests context-dependent flexibility in sleep behavior even within species. Our findings indicate that, even in human-modified environments, animals may maintain ecologically relevant behaviors by selecting suitable microhabitats. These findings build on a growing body of work showing that anoles, like many animals, do not select sleep sites arbitrarily, but instead exhibit consistent spatial behaviors that likely enhance survival during periods of rest. Across taxa, similar sleep site selection strategies have been linked to predation risk, thermal comfort, and light exposure. For example, urban agamid lizards avoid brightly lit perches (Mohanty, Joshi, and Thaker 2021), whereas chimpanzees adjust sleeping height based on predator presence and ambient temperature (Samson and Hunt 2012). These parallels emphasize that sleep is not merely a physiological necessity, but a behavior shaped by ecological and evolutionary pressures. As urbanization and climate change continue to reshape environments, understanding how animals select and use sleep sites will be critical for predicting behavioral resilience. Future work should evaluate whether these patterns hold across systems using both observational and experimental approaches to test the plasticity and constraints of sleep-related behavior in the face of rapid environmental change.

## Author Contributions

**A. Leighanne Sparks:** conceptualization, data curation, formal analysis, writing – original draft, writing – review and editing. **Simon P. Lailvaux:** conceptualization, methodology, supervision, writing – review and editing.

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All procedures involving live animals were approved by the University of New Orleans Institutional Animal Care and Use Committee (IACUC protocol no.: 24-011).

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The authors have nothing to report.

## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All datasets and R code used in this study will be deposited in the Dryad Digital Repository and made publicly available upon publication. For peer review, data can be accessed at the following link: <http://datadryad.org/share/b53yUoHN7ja1kJTqO06dqvgpGLHgh8d1uAf0m7sWCfc>.

## References

Albeck, N., D. I. Udi, R. Eyal, A. Shvartsman, and M. Shein-Idelson. 2022. "Temperature-Robust Rapid Eye Movement and Slow Wave Sleep in the Lizard *Laudakia Vulgaris*." *Communications Biology* 5: 1310. <https://doi.org/10.1038/s42003-022-04261-4>.

Aulsebrook, A. E., F. Connelly, R. D. Johnsson, et al. 2020. "White and Amber Light at Night Disrupt Sleep Physiology in Birds." *Current Biology: CB* 30, no. 18: 3657–3663.e5. <https://doi.org/10.1016/j.cub.2020.06.085>.

Aulsebrook, A. E., R. D. Johnsson, and J. A. Lesku. 2021. "Light, Sleep and Performance in Diurnal Birds." *Clocks and Sleep* 3, no. 1: 115–131. <https://doi.org/10.3390/clockssleep3010008>.

Aulsebrook, A. E., T. M. Jones, N. C. Rattenborg, T. C. Roth, and J. A. Lesku. 2016. "Sleep Ecophysiology: Integrating Neuroscience and Ecology." *Trends in Ecology & Evolution* 31, no. 8: 590–599. <https://doi.org/10.1016/j.tree.2016.05.004>.

Blízquez, M. C., and R. Rodríguez-Estrella. 1997. "Factors Influencing the Selection of Basking Perches on Cardon Cacti by Spiny-Tailed Iguanas (*Ctenosaura hemilopha*)."*Biotropica* 29, no. 3: 344–348. <https://doi.org/10.1111/j.1744-7429.1997.tb00435.x>.

Bors, M., N. P. Mohanty, and P. G. Shankar. 2022. "A Comparison of Daytime and Night-Time Escape Behaviour of the Lizard *Monilesaurus rouxii* (Reptilia: Agamidae)." *Herpetology Notes* 15: 839–844.

Cabrera-Guzmán, E., and V. H. Reynoso. 2010. "Uso de perchas para dormir por la lagartija *Anolis uniformis* (Squamata: Polychrotidae) en el bosque tropical fragmentado de Los Tuxtlas, México." *Revista Mexicana de Biodiversidad* 81, no. 3: 921–924. <https://doi.org/10.22201/ib.20078706e.2010.003.662>.

Campbell-Staton, S. C., K. M. Winchell, N. C. Rochette, et al. 2020. "Parallel Selection on Thermal Physiology Facilitates Repeated Adaptation of City Lizards to Urban Heat Islands." *Nature Ecology & Evolution* 4: 652–658.

Clark, D. L., and J. C. Gillingham. 1990. "Sleep-Site Fidelity in Two Puerto Rican Lizards." *Animal Behaviour* 39, no. 6: 1138–1148. [https://doi.org/10.1016/S0003-3472\(05\)80786-9](https://doi.org/10.1016/S0003-3472(05)80786-9).

Clements, S. L., S. V. L. Catania, and C. A. Searcy. 2019. "Non-Native Species Dominate Herpetofaunal Community Patterns in Both Native and Non-Native Habitat Patches in Urban Miami-Dade County." *Biological Invasions* 21, no. 5: 1757–1770. <https://doi.org/10.1007/s10530-019-01934-w>.

Delaney, D. M., and D. A. Warner. 2016. "Age- and Sex-Specific Variations in Microhabitat and Macrohabitat Use in a Territorial Lizard." *Behavioral Ecology and Sociobiology* 70: 981–991. <https://doi.org/10.1007/s00265-016-2121-3>.

Eban-Rothschild, A., W. J. Giardino, and L. de Lecea. 2017. "To Sleep or Not to Sleep: Neuronal and Ecological Insights." *Current Opinion in Neurobiology* 44: 132–138.

Edwards, J. R., and S. P. Lailvaux. 2012. "Display Behavior and Habitat Use in Single and Mixed Populations of *Anolis carolinensis* and *Anolis sagrei* Lizards." *Ethology* 118, no. 5: 494–502. <https://doi.org/10.1111/j.1439-0310.2012.02037.x>.

Feilen, K. L., and A. J. Marshall. 2014. "Sleeping Site Selection by Proboscis Monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia." *American Journal of Primatology* 76, no. 12: 1127–1139. <https://doi.org/10.1002/ajp.22298>.

Fetters, T. L., and J. W. McGlothlin. 2017. "Life Histories and Invasions: Accelerated Laying Rate and Incubation Time in an Invasive Lizard, *Anolis sagrei*." *Biological Journal of the Linnean Society* 122, no. 3: 635–642. <https://doi.org/10.1093/biolinnean/blx102>.

Glass, T. W., G. A. Breed, M. D. Robards, C. T. Williams, and K. Kielland. 2021. "Trade-Off Between Predation Risk and Behavioural Thermoregulation Drives Resting Behaviour in a Cold-Adapted Mesocarnivore." *Animal Behaviour* 175: 163–174. <https://doi.org/10.1016/j.anbehav.2021.02.017>.

Helfrich-Förster, C. 2017. "Sleep in Insects." *Annual Review of Entomology* 63: 69–86.

Husak, J. F., and S. P. Lailvaux. 2019. "Experimentally Enhanced Performance Decreases Survival in Nature." *Biology Letters* 15, no. 4: 20190160. <https://doi.org/10.1098/rsbl.2019.0160>.

Huey, R. B. 1974. "Behavioral Thermoregulation in Lizards: Importance of Associated Costs." *Science* 184, no. 4140: 1001–1003. <https://doi.org/10.1126/science.184.4140.1001>.

Huey, R. B. 1991. "Physiological Consequences of Habitat Selection." *American Naturalist* 137: S91–S115.

Irschick, D. J., E. Carlisle, J. Elstrott, et al. 2005. "A Comparison of Habitat Use, Morphology, Clinging Performance, and Escape Behaviour Among Two Divergent Green Anole Lizard (*Anolis carolinensis*) Populations." *Biological Journal of the Linnean Society* 85: 223–234. <https://doi.org/10.1111/j.1095-8312.2005.00487.x>.

Irschick, D. J., and J. B. Losos. 1999. "Do Lizards Avoid Habitats in Which Performance Is Submaximal? The Relationship Between Sprinting Capabilities and Structural Habitat Use in Caribbean Anoles." *American Naturalist* 154: 298–305.

Irschick, D. J., M. Ramos, J. Buckley, et al. 2006. "Are Morphology-Performance Relationships Invariant Across Different Seasons? A Test With the Green Anole Lizard (*Anolis carolinensis*)."*Oikos* 114, no. 1: 49–59. <https://doi.org/10.1111/j.2006.0030-1299.14698.x>.

Irschick, D. J., B. Vanhooydonck, A. Herrel, and J. J. Meyers. 2005. "Intraspecific Correlations Among Morphology, Performance, and Habitat Use Within a Green Anole Lizard (*Anolis carolinensis*) Population." *Biological Journal of the Linnean Society* 85: 211–221.

Johnson, D. H. 1980. "The Comparison of Usage and Availability Measurements for Evaluating Habitat Preference." *Ecology* 61: 65–71.

Kolbe, J. J., R. E. Glor, L. R. Schettino, A. C. Lara, A. Larson, and J. B. Losos. 2004. "Genetic Variation Increases During Biological Invasion by a Cuban Lizard." *Nature* 431: 959–960.

Kolbe, J. J., H. A. Moniz, O. Lapiendra, and C. J. Thawley. 2021. "Bright Lights, Big City: An Experimental Assessment of Short-Term Behavioral and Performance Effects of Artificial Light at Night on *Anolis* Lizards." *Urban Ecosystems* 24, no. 5: 1035–1045. <https://doi.org/10.1007/s11252-021-01098-3>.

Lailvaux, S. P. 2020. "It's Not Easy Being Green: Behavior, Morphology, and Population Structure in Urban and Natural Populations of Green Anole (*Anolis carolinensis*) Lizards." *Frontiers in Ecology and Evolution* 8: 570610.

Libourel, P. A., B. Barrillot, S. Arthaud, et al. 2018. "Partial Homologies Between Sleep States in Lizards, Mammals, and Birds Suggest a Complex Evolution of Sleep States in Amniotes." *PLoS Biology* 16, no. 10: e2005982. <https://doi.org/10.1371/journal.pbio.2005982>.

Lima, S. L., N. C. Rattenborg, J. A. Lesku, and C. J. Amlaner. 2005. "Sleeping Under the Risk of Predation." *Animal Behaviour* 70: 723–736.

Losos, J. B., J. C. Marks, and T. W. Schoener. 1993. "Habitat Use and Ecological Interactions of an Introduced and a Native Species of *Anolis* Lizard on Grand Cayman, With a Review of the Outcomes of Anole Introductions." *Oecologia* 95: 525–532.

Losos, J. B., and C. J. Schneider. 2009. "Anolis Lizards." *Current Biology* 19, no. 8: R316–R318. <https://doi.org/10.1016/j.cub.2009.02.017>.

Mohanty, N. P., S. Harikrishnan, and K. Vasudevan. 2016. "Watch Out Where You Sleep: Nocturnal Sleeping Behaviour of Bay Island Lizards." *PeerJ* 4: e1856. <https://doi.org/10.7717/peerj.1856>.

Mohanty, N. P., M. Joshi, and M. Thaker. 2021. "Urban Lizards Use Sleep Sites That Mirror the Structural, Thermal, and Light Properties of Natural Sites." *Behavioral Ecology and Sociobiology* 75, no. 12: 1–11. <https://doi.org/10.1007/s00265-021-03101-5>.

Mohanty, N. P., C. Wagener, A. Herrel, and M. Thaker. 2021. "The Ecology of Sleep in Non-Avian Reptiles." *Biological Reviews* 97: 505–526.

Poche, A. J., Jr., R. O. Powell, and R. W. Henderson. 2005. "Sleep-Site Selection and Fidelity in Grenadian Anoles." *Herpetazoa* 18: 3–10.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. <https://www.R-project.org>.

Raap, T., R. Pinxten, and M. Eens. 2015. "Light Pollution Disrupts Sleep in Free-Living Animals." *Scientific Reports* 5: 13557.

Samson, D. R., and K. D. Hunt. 2012. "A Thermodynamic Comparison of Arboreal and Terrestrial Sleeping Sites for Dry-Habitat Chimpanzees (*Pan troglodytes schweinfurthii*) at the Toro-Semliki Wildlife Reserve, Uganda." *American Journal of Primatology* 74, no. 9: 811–818. <https://doi.org/10.1002/ajp.22031>.

Singhal, S., M. A. Johnson, and J. T. Ladner. 2007. "The Behavioral Ecology of Sleep: Natural Sleeping Site Choice in Three *Anolis* Lizard Species." *Behaviour* 144, no. 9: 1033–1052.

Spoelstra, K., and M. E. Visser. 2014. "The Impact of Artificial Light on Avian Ecology." In *Avian Urban Ecology*, edited by D. Gil and H. Brumm, 21–28. Oxford University Press.

Walguarnery, J. W., R. M. Goodman, and A. C. Echternacht. 2012. "Thermal Biology and Temperature Selection in Juvenile Lizards of Co-Occurring Native and Introduced *Anolis* Species." *Journal of Herpetology* 46, no. 4: 620–624.

Weaver, R. E. 2011. "Effects of Simulated Moonlight on Activity in the Desert Nightsnake (*Hypsiglena chlorophaea*)."*Northwest Science* 85, no. 3: 497–500. <https://doi.org/10.3955/046.085.0308>.

Weber, W. D., N. M. Anthony, and S. P. Lailvaux. 2021. "Size but Not Relatedness Drives the Spatial Distribution of Males Within an Urban Population of *Anolis carolinensis* Lizards." *Ecology and Evolution* 11, no. 6: 2886–2898. <https://doi.org/10.1002/ece3.7248>.

Williams, E. E. 1983. "Ecomorphs, Faunas, Island Size, and Diverse End Points in Island Radiations of *Anolis*." In *Lizard Ecology: Studies of a Model Organism*, edited by R. B. Huey, E. R. Pianka, and T. W. Schoener. Harvard University Press.

Winchell, K. M., I. Maayan, J. R. Fredette, and L. J. Revell. 2018. "Linking Locomotor Performance to Morphological Shifts in Urban Lizards." *Proceedings of the Royal Society B: Biological Sciences* 285: 10.