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Sleeping behavior, sleep duration, and the sleep–wake transition in two species of Puerto Rican anoles

Steven Poe & Thomas L. Kennedy

Department of Biology, University of New Mexico, Albuquerque, New Mexico, 87131 USA

Corresponding author: Steven Poe, e-mail: anolis@unm.edu

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Abstract. Sleeping behavior across the diel period is understudied in squamates. We documented behavior during sleep and the sleep–wake transition in an assemblage of *Anolis* lizards (anoles) in Puerto Rico. We performed both field population surveys and longitudinal studies of individuals overnight. Fifty-six of 59 individuals tracked longitudinally chose an arboreal sleeping perch on light vegetation at sundown and stayed nearly or completely motionless on that perch until sunrise. Sleep duration in *A. cristatellus* and *A. krugi* was 12 to 13 hours across species and individual/population studies, an interval that corresponded to the dark nighttime period. Diel transitions between sleep and wakefulness were found to be brief; in the extreme case of the change between sleeping to wakefulness recorded in our population study, the period wherein both sleeping and wakeful anoles was observed was just two to eight minutes. Anoles in our studied assemblage were extraordinarily scarce during a brief, ~1 hour period after sleep and before daytime active behavior. This "morning retreat," possibly involving hiding in or below vegetation, may reflect antipredator behavior whereby an ectotherm becomes secretive while compromised due to overnight sleep and before basking is sufficiently beneficial for emergence.

Key words. Squamata, Sauria, Anolidae, *Ctenonotus* clade, lizards, sleep site, vertebrates.

Introduction

Sleep is a ubiquitous and temporally significant state in animals, but behavioral information on sleep and the sleep–wake transition is lacking for most reptile species. In squamates, fewer than one percent of the 11000+ species have been studied for basic sleep characteristics such as sleep duration or sleeping posture (s. Libourel & Herrel 2016 and Mohanty et al. 2022 for reviews). Mammals and birds have been surveyed for sleep behaviors much more thoroughly than squamates (e.g., Allison & Cichetti 1976, Amlaner & Ball 1983, Elgar et al. 1988, Siegel 2005, Rattenborg & Martinez-Gonzalez 2015). If the study of sleep is to be comparative, both within squamates and across animals, information on the sleeping behaviors of squamate species is needed.

Fundamental characteristics of sleep are duration and particular diel period. Differences in sleep duration are apparent across mammals and birds, allowing some comparative analyses (e.g., Elgar et al. 1988), but have been much less chronicled in squamates. The few squamate species that have been studied rigorously were shown to sleep from 4.2 (*Iguana iguana*) to 20.4 hours (*Python sebae*) per diel cycle, generally at night (Campbell & Tobler 1984). In many squamate species there is some anecdotal, indirect, and/or individual evidence for an approximately dark/night sleep/wake cycle (e.g., Rand 1967), but several species including geckos are known to be active nocturnally (Pianka & Vitt 2003). Many squamate species concentrate nearly all sleep in a particular cycle, often nighttime, whereas others sleep intermittently during the diel cycle (Campbell & Tobler 1984). Among squamates, crepuscular forms such as some rattlesnakes (e.g., Degenhardt et al. 1996) qualify as intermittent diel sleepers. Each of the above sleep characteristics may vary ontogenetically, sexually, seasonally, or individually (e.g., Steinmeyer et al. 2010), for example in diurnal snakes becoming crepuscular during hot periods (e.g., Shine 1987).

Anolis (anoles) are perhaps the best studied squamates for sleeping perch (examples: Kattan 1984, Goto & Osborne 1989, Singhal et al. 2007, Cabrera-Guzman & Reynoso 2010). But anole sleep duration, awakening behavior, and overnight sleeping behaviors have not been studied beyond inferences from brief observation (see e.g. Rand 1967). Like many arboreal lizard species, anoles tend to sleep exposed on twigs or leaves (e.g., Schwartz & Henderson 1991), presumably to facilitate detection of nocturnal predators such as arboreal snakes that may jiggle the lizard's sleeping perch while approaching (Bors et al. 2020). Here we study sleeping and wakeful behavior in an assemblage of anoles in nature in Puerto Rico. We document sleep duration and behavior in individual anoles and assess population-level behavior across the diel transitions.

Materials and methods

Assessment of the wake–sleep–wake cycle in an assemblage of anoles

We undertook field observations at a farm at Carite Lake in Guayabo, Puerto Rico (18.064, -66.091, 570 m, from 12 December 2022 until 15 December 2022. One of us (SP) surveyed the grounds for *Anolis* lizards from 16:10 until 21:00 and from 5:15 to 8:30 for three consecutive overnights. The farm includes trails through disturbed and secondary forests and a road through open highly disturbed areas. To determine sleep–wake cycles, each trail and the road was surveyed for anoles twice, once at night and once during the day. Lizards were searched for on vegetation and the ground, focusing on lower perches because anoles were most easily detectable in those areas. The time of first sighting of each observed lizard was recorded. During the night surveys, a bright light was used to find sleeping lizards.

Each observed individual was categorized as either active or sleeping. Individuals were recorded to be *active* if they were moving when first seen or fled when approached, or if they were clearly in an awakened stance (i.e., head and body lifted above substrate). Individuals were recorded to be *sleeping* if they remained motionless in a posture flush with substrate, even upon close approach, i.e., they did not respond evasively before attempted capture. Eye closure was not included in our sleep categorization because many individuals would open their eyes upon discovery, presumably in response to the light trained on them, but still would remain motionless upon observer approach, reclosing eyes if left alone (this lack of wariness disqualifies our 'sleeping' individuals from being categorized as 'pseudo-sleepers' sensu Amlaner & McFarland 1981).

Note that our sleep criteria generally meet behavioral standards for sleep, including those based on Pieron's (1913) criteria. That is, they cover individuals that are in a stereotypic posture (chin and body flush with substrate, with limbs and body arranged in positions not generally observed in awake individuals), engaged in behavioral quiescence with an elevated arousal threshold (remaining motionless even upon observer approach), in a state that is reversible with stimulation (if sleeping perch is strongly disturbed, lizards drop or flee). The few anoles that were observed but could not be categorized according to the above awake/asleep definitions – < 1% observations – were not included in this study. Active individuals were identified to genus (i.e., *Anolis*) but not species; sleeping individuals were identified to species. Data on sex, perch height and substrate (e.g., leaf vs. twig vs. grass), and body length (snout to vent length, SVL) were taken on sleeping individuals.

For each morning, we took the median of time of first awake individual observed and time of last asleep individual observed as an estimate of central tendency of time of becoming awake for the population. The reverse was done each evening (i.e., first asleep, last awake) to obtain an estimate for time of beginning sleep.

Sleeping behavior assessed longitudinally in individuals

For three overnights at the Carite Lake site one of us (TK) surveyed a short transect from 18:40 to 22:30 at approximately 30-minute intervals, and from 05:30 until surveyed anoles were no longer visible. During the initial survey at 18:40, sleeping anoles were located and photographed, and the perch of each photographed anole was marked with pink tape. During subsequent surveys TK took photos of the same documented sleeping perches to produce a time-series of sleeping behavior for individuals overnight. Photos were later evaluated to chronicle overnight behavior and estimate time of waking.

Results

The anole assemblage at Carite Lake

Sunset was at approximately 17:50 and sunrise at 6:47 during our field studies. Four species were seen commonly during day and night: *Anolis cristatellus, A. evermanni, A. stratulus,* and *A. krugi.* However, given our survey designs focused on lower, highly visible individuals, the bulk of our data observations were of *A. krugi* and *A. cristatellus.* Thus, our results mainly concern the behaviors of these two species. Anoles were highly abundant during daytime and nighttime, with rates of observation greater than one individual per minute occurring during many 20-minute daytime segments and of multiple individuals per minute during some 20-minute nighttime segments. Rate of recorded nighttime observations was limited by the extensive data collected for sleeping individuals (see Methods). Anoles observed in this study slept with limbs flexed or extended, with body aligned vertically or horizontally and stretched out elongate or curled up. See Figure 1 for examples of sleeping individuals.

Sleeping *Anolis krugi* perched at = 0.92 m (SD = 0.50, n = 123) above ground, mainly on leaves or grasses (88%). Sleeping *A. cristatellus* perched at = 1.11 m (SD = 0.85, n = 88) above ground on leaves/grasses (81%) or twigs (19%). Our few nighttime observations of *A. stratulus* (mean perch height = 1.5 m, perch substrate = 83% leaf, n = 6) and *A. evermanni* (mean perch height = 8.5 m, perch substrate = 100% leaf, n = 2) were of higher-perching individuals than *A. cristatellus* and *A. krugi.*

The anole assemblage overnight

During an extended nighttime period (18:11–6:16, 18:08–6:22, 18:30–6:12 for the three nights), all observed anoles were found sleeping on leaves, grasses, stems, or twigs, staying immobile even upon close approach (n = 232 individuals observed). No anoles were sighted on tree trunks, thick branches, rocks, walls, or the ground during these periods. During an extended daytime period (6:19–17:42, 7:36–18:29, 6:21–8:30), anoles invariably were

Table 1. Summary of time of first observed sleeping and wakeful anole, last observed sleeping and wakeful anole, for three diel cycles in an assemblage of *Anolis* in Puerto Rico. Time asleep is calculated from population estimates of retiring and waking (see Materials and methods).

Cycle	Sunset/ nautical twilight	first asleep	last awake	summary retire	Nautical twilight/ sunrise	first awake	last asleep	summary awaken	Time asleep
12/13	17:50/18:40	17:47	18:08	17:58	5:56/6:46	6:18	6:19	6:19	12:21
13/14	17:51/18:40	17:43	18:05	17:54	5:57/6:47	6:29	6:32	6:31	12:37
14/15	17:51/18:40	18:05	18:29	18:17	5:57/6:47	6:13	6:20	6:17	12:00

found to be active, fleeing when approached (n = 284). During daytime many anoles were observed on tree trunks, thick tree branches, walls, and the ground, in addition to leaves and twigs. The period during which we observed some awake and some sleeping lizards was brief during all six observed diel transitions (3 around sunrise, 3 around sunset), extending from two to eight minutes in the morning and 22–25 minutes in the evening (Fig. 2). Neither *A. cristatellus* nor *A. krugi* consistently awakened or retired earlier than the other species. Observed retiring and waking times for the populations are summarized in Table 1.

The transition between observations of sleeping and wakeful anoles included an extended period during which anole detectability was very low (Fig. 2). Relatively few anoles were seen each morning after anoles ceased to be observed on sleeping perches and before they reappeared and were active: three anoles in 99 minutes (6:33–8:12; 0.03 anoles/minute) were observed on the morning of 13 December, zero anoles in 62 minutes (6:33–7:35; 0.0 anoles/minute) were observed on the morning of 14 December, one anole in 49 minutes (6:38–7:26; 0.02 anoles/minute) was observed on the morning of 15 December. Following each of these periods, much higher diurnal anole detection rates were recorded until 8:30, when surveys were suspended (0.71 anoles/minute for 13 December, 0.19 anoles/minute for 14 December, 0.37 anoles/minute for 15 December).

Figure 1. Examples of sleeping anoles. (A, B) *Anolis krugi* and (C, D) *A. cristatellus*.

Longitudinal study of individual anoles

We recorded time series photographs for 59 anoles perching from nighttime to morning (12–13 December: n = 13, 13–14 December: n = 24, 14–15 December: n = 22; n = 31 *A. cristatellus,* n = 28 *A. krugi;* Table 2). In a few cases, we were unable to refind perches during searches; these cases are not discussed further. Among anoles at 59 tracked perches, three individuals vacated perches overnight, one for an alternative perch within one meter of the initial perch and two that could not be found again. The remaining 56 anoles (94.9%) remained at their initial sleeping perches from initial observation until waking at dawn. Among these individuals, 35 (62.5%) were completely motionless overnight and 17 (30.4%) slightly adjusted their position, where a 'slight' adjustment was marked when those individuals moved a limb or the head without body repositioning. Four individuals (7.1%) reversed or otherwise greatly altered their body positions overnight.

Time of awakening for each individual was estimated as the median of last time observed asleep and first time observed awake. In most cases, this interval was less than 20 minutes (Table 2). The few cases for which waking interval could not be narrowed down in this way (e.g., because individuals appeared awake when first observed in the morning) were discarded in our estimates of waking time. Of 46 individuals for which time of awakening could be estimated, mean time of awakening was 6:08 (SD = 20 minutes; Table 2).

Discussion

Sleep period and duration

Anoles in our studied assemblage were found to sleep constantly during darkness, from several minutes before sundown until nearly sunup, with only minor shifts in body movement overnight. The consistency of the conclusion of constant nighttime sleep across two species of *Anolis* and both longitudinal and population studies is evidence for the veracity of this inference (Whewell 1840), at least for these two species for this site but hypothetically for the entire anole clade (pers. obs. of thousands of anoles; Table 1, 2; Figs 2, 3).

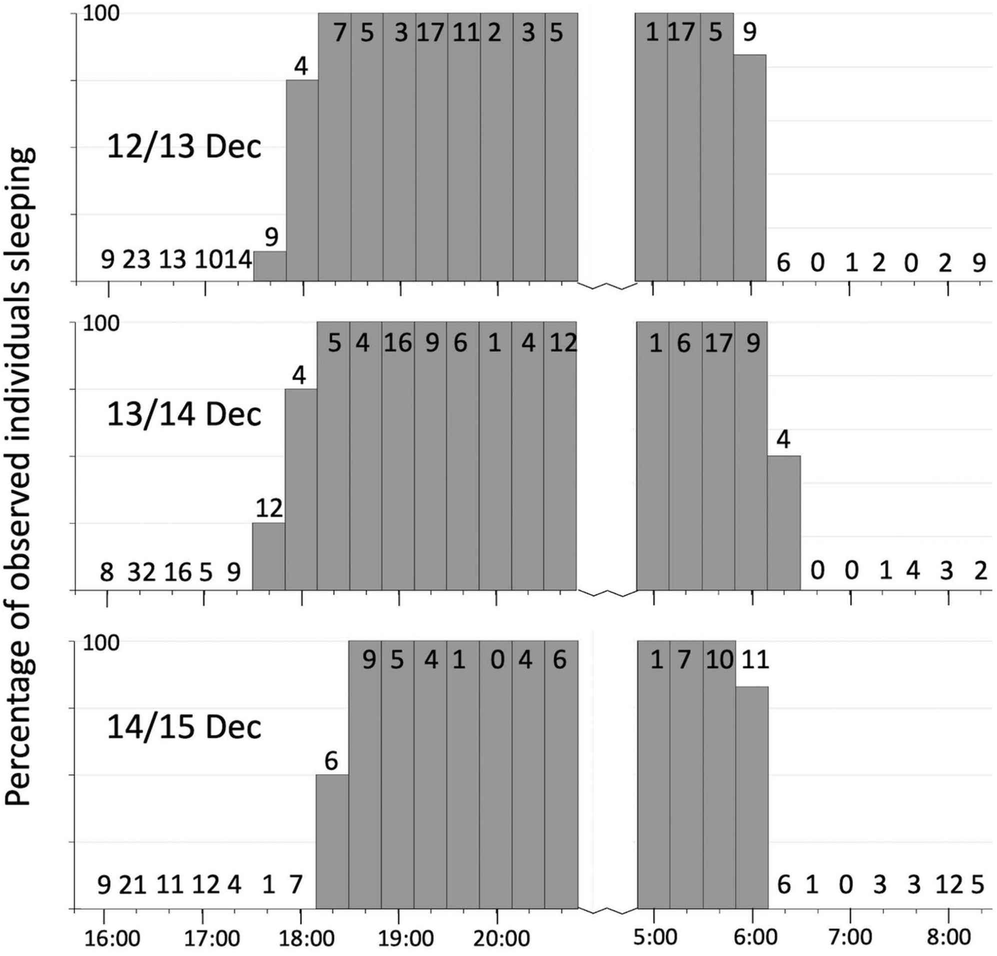

Figure 2. Data from evening and morning surveys. Bars correspond to 20-minute time intervals. Numbers above bars are number of anoles observed in the corresponding time interval.

Table 2. Longitudinal time sequences taken from snapshots of individual lizards observed sleeping. Data from *Anolis cristatellus* are labeled crist, data from *A. krugi* are labeled krugi. Listed times are when individuals were photographed. An "A" indicates that the observed individual was categorized as awake, a "S" indicates the observed individual was categorized as sleeping. An asterisk (*) signals a minor change in body positioning relative to last observation (e.g., slight change in foot position). Two asterisks signals a major change in body position relative to last observation (e.g., reversal of body position). Approximate time of awakening is calculated as the median time of last sleeping and first awake observation.

		Date	Evening observations	Morning observations	Appr. awakening	Confirmed absent from perch
crist	3.2	14.15/12/2022	18:36S, 1930S, 20:30S, 21:31S, 22:30S	5:19S, 6:00S, 6:28A*, 6:44A*	6:14	7:01
krugi	3.3	14.15/12/2022	18:38S, 19:31S, 20:31S, 21:32S, 22:31S	5:20S*, 6:00S, 6:29A**	6:15	6:44
crist	3.4	14.15/12/2022	18:40S, 19:31S*, 20:32S, 21:32S, 22:31S*	5:20S*, 6:00A*, 6:29A*	5:50	6:44
crist	3.5	14.15/12/2022	18:41S, 1936S**, 20:32**, 21:32*, 22:32*	5:20S, 6:01A	6:01 (observed waking)	6:29
krugi	3.6	14.15/12/2022	18:42S, 19:32S, 20:32S, 21:32S*	6:01A*, 6:29A**	before 6:01	6:45
krugi	3.7	14.15/12/2022	19:32S, 20:32S, 21:32S, 22:32S	5:20S*, 6:01S	6:14	6:30
krugi	3.8	14.15/12/2022	18:42S, 19:32S, 20:32S, 21:33S, 22:32S,	5:20S, 6:01S	6:14	6:30
krugi	3.9	14.15/12/2022	18:43S, 19:33S, 20:33S, 21:33S, 22:33S	5:21S, 6:01S, 6:30S	6:37	6:45
crist	3.10		18:44S, 19:33S, 20:33S, 21:34S, 22:38S	5:21S, 6:02A*, 6:30A**, 6:45A	5:41	7:02
crist	3.11		18:46S, 19:33S, 20:33S, 22:34S	Absent from perch	?	?
krugi	3.12		18:47S, 19:34S, 20:33S, 21:34S, 22:33S	5:25S, 6:02S, 6:30S	6:37	6:45
krugi	3.13		18:47S, 109:33S, 20:33S, 21:34S, 22:33S,	5:25A**, 6:02A	before 5:25	6:30
krugi	3.14		18:48S, 19:34S, 20:34S, 21:34S, 22:34S	5:25S, 6:03S	6:17	6:31
krugi	3.15		18:51S, 19:34S, 20:34S, 21:35S, 22:34S,	6:03S	6:17	6:31
krugi	3.16		18:51S, 19:35S, 20:35S, 21:35S	5:25S, 6:03S, 6:31S	6:38	6:45
crist	3.17		18:52S, 19:35S, 20:35S, 21:36S, 22:34S	6:03S	6:17	6:31
crist	3.18		18:53S, 19:35S, 20:35S, 21:36S, 22:35S	5:21S, 6:03S, 6:31A*, 6:46A**	6:17	7:03
krugi	3.19		18:53S, 19:35S, 20:35S, 21:36S, 22:35S	5:26S, 6:04A*	5:45	6:32
crist	3.20		18:55S, 19:36S, 20:36S, 21:36S, 22:35S	5:26S, 6:05A**	5:45	6:32
crist	3.21		18:57S, 19:36S, 20:36S, 21:36S, 22:36S	5:26S, 6:04A*, 6:32A*	5:44	6:47
crist	3.22		18:58S, 19:36S, 20:36S, 21:37S, 22:36S	5:27S, 6:04S, 6:32S	6:39	6:47
crist	3.23		18:59S, 19:37S, 20:36S, 21:37S, 22:36S	5:27S*, 6:05S	6:18	6:32
crist	2.2		22:30S	5:18S*, 6:00A*, 6:24A*, 6:35A	5:39	6:42
krugi	2.5		21:34S, 22:31S	5:19S, 6:01S, 6:25A*	6:13	6:35
crist	2.6		18:40S, 19:33S, 20:32S, 213:34S, 22:31S	5:20A*, 6:03A*, 6:26A**, 6:36A*, 6:43A, 6:50A, 7:02A*	before 5:20	7:02+
krugi	2.7		18:42S, 19:35S, 21:34S, 22:32S	5:21S, 6:27A*	5:54	6:36
krugi	2.10		20:33S, 21:35S, 22:32S	5:21S, 6:03S, 6:27S*	6:32	6:36
krugi	2.11		20:33S, 22:33S	5:22S, 6:03S, 6:27S	6:33	6:37
krugi	2.12		18:43S, 19:37S, 20:33S, 21:35S, 22:33S	5:23S, 6:04S	6:16	6:28
crist	2.13		18:44S, 19:38S, 20:34S, 21:36S, 22:33S	5:24S, 6:05A*, 6:28A**, 6:42A*,6:51A**	5:44	?
krugi	2.15		22:34S	5:25S, 6:06*A	5:47	6:29
krugi	2.16		22:34S	5:35A*, 6:06A**	before 5:35	?
krugi	2.17		22:35S	5:25S*, 6:06S, 6:29S, 6:38S	after 6:38	?
krugi	2.18		18:49S, 19:41S, 21:38S, 22:35S	5:26S**, 6:06S	6:18	6:29
crist	2.19		18:50S, 19:42S, 20:35S, 21:38S, 22:36S	5:28S*, 6:07S*	6:19	6:30
crist	2.20		18:51S, 19:45S, 20:37S, 21:39S, 22:36S	5:28S, 6:07S	6:19	6:30
krugi	2.21		18:55S, 20:38S, 21:39S, 22:36S	5:29S, 6:08S, 6:30A	6:20	6:30+
crist	2.22		18:55S, 19:46S, 20:39S, 21:39S, 22:37S,	5:29S*, 6:08A**	5:48	6:30
crist	2.23		18:56S, 19:46S, 20:39S, 21:39S, 22:37S	5:29S, 6:08S, 6:31S*, 6:40S, 6:45S	6:48	6:51
krugi	2.24		19:46S, 20:39S, 21:40S, 22:37S	5:30S, 6:09A*	5:49	6:31

Table 2 continued

		Date	Evening observations	Morning observations	Appr. awakening	Confirmed absent from perch
crist	2.25		18:59S, 19:47S, 20:40S, 21:40S, 22:38S	5:30S**, 6:09S	6:20	6:32
krugi	2.26		19:03S, 19:49S, 20:40S, 21:41S, 22:39S	5:31S*, 6:09S	6:20	6:31
krugi	2.27		19:04S, 19:49S, 21:42S, 22:41S	Absent from perch	?	?
crist	2.28		20:41S	5:31A (different leaf)	before 5:31	?
crist	2.29		19:04S, 19:49S, 20:41S, 21:41S, 22:58S	5:31S, 6:40A	6:06	?
crist	2.30	13.14/12/2022	20:42S, 21:42S, 22:41S	5:32S, 6:11A*	5:51	6:34
crist	1.1	12.13/12/2022	18:41S, 19:23S, 20:26S, 21:54S, 23:00S	5:13S, 5:41S, 5:58A*, 6:16S*, 6:32S*, 7:06A*	5:49	7:15
krugi	1.2		18:42S, 19:25S, 20:35S, 23:02S	5:16S*, 5:41S, 6:00S, 6:16S	6:15	6:30
krugi	1.3		18:43S, 19:27S, 20:30S, 10:01S, 11:01S	5:17S, 5:42A*, 6:00A, 6:17A, 6:33A*	5:30	6:45
crist	1.4		18:45S, 19:30S, 20:39S, 22:09S, 23:08S	5:22S, 5:47S*, 6:05S	6:11	6:17
crist	1.7		18:47A, 20:42S*, 22:14S, 23:11S	5:25S*, 5:50A**, 6:08A**	5:38	6:17
crist	1.9		18:49S, 19:36S, 20:46S, 22:19S, 23:15S*	5:31S*, 6:11S	after 6:11	?
crist	1.10		18:49S, 20:46S, 22:19S, 23:16S	6:132A**	6:12-	
crist	1.11		19:26S, 21:28S, 21:58S**	6:00S	6:00+	?
crist	1.12		19:26S, 20:30S, 22:00S, 23:01S	5:17A*, 5:42A**	5:17-	?
krugi	1.18		23:10S	5:48S, 6:06S, 6:22A*	6:14	?
crist	1.20		23:08S	5:23S*, 5:48A**, 6:06A*, 6:21A*, 6:45A*	5:36	?
krugi	1.21		20:45S	5:54S, 6:11S, 6:26S	6:26+	?
crist	1.26		23:05S	5:18S*, 5:44S, 6:01S*, 6:18A*	6:10	?

Phylogenetic assessment of the approximately 12 to 13 hour nighttime sleep duration for our studied anoles within squamates is not straightforward given the differences in methodology employed in sleep duration research. Our study is purely behavioral and undertaken mainly at night, with no electrophysiological aspect and no monitoring of potential sleep states during daytime. That is, our methodology allowed us to test neither physiological indicators of sleep nor whether individuals nap during the day. Notwithstanding these caveats, anoles appear to sleep less than *Dipsosaurus dorsalis* (16.3 h to 17.8 h; Huntley et al. 1977), more than *Iguana iguana* (4.2–7.9 h; Flanigan 1973), and perhaps comparably to *Phrynosoma regali* (12.3 h; Romo et al. 1978) per diel cycle. Lizard species that have been shown to move towards sleep sites around dusk (e.g., *Agama agama* [Amadi et al. 2020], *Psammophilus dorsalis* [Mohanty et al. 2021], *Anolis lineatopus* [Rand 1967]) likely share at least an approximate dark/light sleep/wake schedule with our studied anoles. But until standardized studies of multiple taxa occur such inferences, and the causes of differences in sleep duration, will remain unresolved.

Overnight sleeping behavior

Our results show that anoles choose a sleeping site and then display site fidelity throughout the night. This conclusion (e.g., Clark & Gillingham 1990) confirms an assumption of many field studies of lizard sleep and underscores the importance of lizards choosing a favorable sleeping site (e.g., Rand 196, Goto & Osborne 1989). Lizards may choose a sleeping site based on hydric or thermal properties (e.g., Christian et al. 1984) or resistance to predation (reviewed in Mohanty et al. 2022). Likewise, the motionlessness or nearly motionlessness of individuals we observed over the entire night may be a strategy to avoid detection by predators (Meddis 1975). The thermal favorability of chosen sleep sites has been shown for some lizard species (e.g., Huey et al. 1989, Pereira et al. 2019) but to our knowledge differences in predation vulnerability of alternative sites have not yet been tested for arboreal lizards. However, the theoretical value of insubstantial sleep perches (twigs, leaves) for predator avoidance in arboreal lizards is clear (Singhal et al. 2007, Mohanty et al. 2022). Indirect evidence of predation effect on sleeping perch occurs in the selection of plausibly safer body orientations for sleep (e.g., Kattan 1984, Clark & Gillingham 1990, Cabrera-Guzman & Reynoso 2010, but see Shew et al. 2002, Vitt et al. 2003a, b). Given that 56 of 59 anoles we observed maintained their positions overnight, a maximum of 3/59 anoles were subject to disturbance such as a predation attempt that prompted vacation of perch.

Overnight immobility or near immobility was observed among almost all individuals tracked overnight. However, sleeping position was variable between and within species in our study. Some other work has shown stereotypical sleeping positions within anole species (e.g., Clark & Gillingham 1990, Storks & Leal 2020). We suggest that perch substrate is an additional determinant of sleeping position in anoles, with individuals often sleeping with limbs extended on narrow perches and with limbs flexed on broad perches (e.g., Fig. 1). The well-established diurnal microhabitat specializations of anoles (e.g., Collette 1961), if also present nocturnally, could lead to species-specific sleeping postures in anoles.

Diel transitions

The diel transitions of the Lake Carite anole population occurred during very brief windows of time (Table 1). Most extremely, the transition from sleeping to wakefulness in the population study happened during a mere one-to-seven minute period. That is, the time during which both sleeping and wakeful anoles were observed in the morning was, at maximum, eight minutes (but see Results of longitudinal study). This result suggests a common trigger for waking across this anole population. It does not conclusively implicate either endogenous or environmental factors.

Our observations of diel transitions in the population study necessarily occurred over particular areas of our study site. We obviously could not survey our entire study area during sunrise or sunset simultaneously given our experimental design, and certainly the assemblage-wide variability in diel transition time and duration is larger than the 1 to 7 minute range we observed here. To wit, the range from earliest to latest time of waking among all individuals across three nights in the longitudinal study is approximately an hour (compare approximate awakening times across individuals in Table 2). Anecdotally, we noticed some possible minor differences in the timing of retiring anoles according to the shadiness of the habitat. That is, anoles seemed to retire earlier in darker shady habitats than in more open habitats, a behavior more consistent with environmental (i.e., light and/or temperature) factors as driving diel behaviors. We note that one of the trials, overnight 2, included significant rain in the evening but during the other two trials the weather was clear, and yet quite similar results for the diel period and length of diel transition were obtained in all three trials (Table 1).

Anoles retired in twilight before complete darkness, and awakened at twilight when the environment was light, before full sun but well after complete darkness. These re-

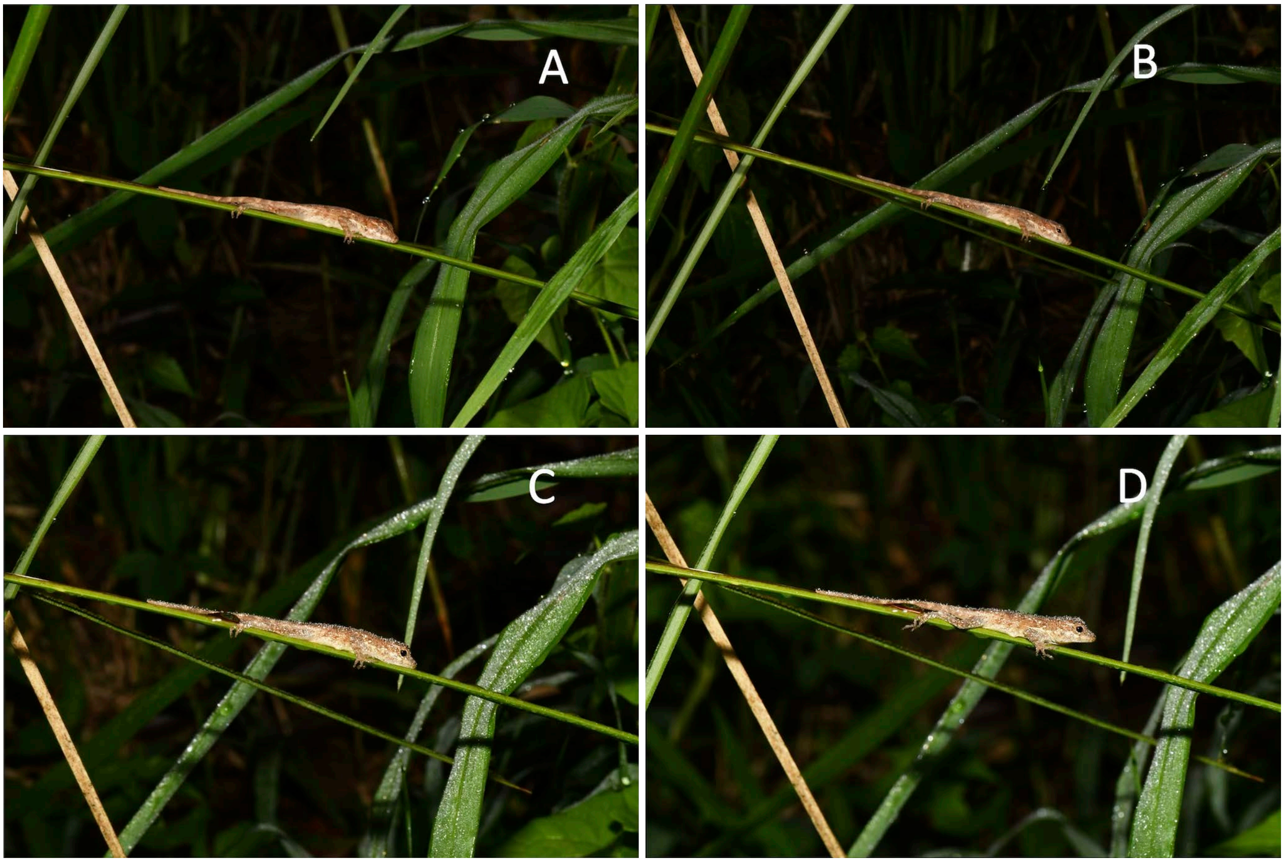

Figure 3. A longitudinal snapshot sequence of one *Anolis krugi* sleeping overnight. Asleep at (A) 20:26, (B) 23:00, and (C) 5:41 (the individual was awakened by the light and stayed stationary); (D) awake at 5:58. This individual occupied the perch until at least 7:06 and was absent at 7:15.

sults differ from those obtained for the arboreal diurnal gecko *Lygodactylus tolampyae,* which occupies nighttime sleeping perches of twigs and leaves like anoles but vacates those perches while the environment is still dark (Ikeuchi et al. 2012). Ikeuchi et al. (2012) interpreted this pre-dawn movement as a pre-emptive defense against early diurnal predators. We found anoles to be nearly undetectable, presumably hiding under low vegetation, during an approximately one-hour time window occurring after sleep and before observable activity (Fig. 2). This "morning retreat" may serve a somewhat similar early diurnal antipredatory function to the pre-dawn activity of *L. tolampayae*. That is, secretive behavior in early morning, when ectothermic individuals are compromised due to cold-induced post-sleep torpor before full sun imparts energy via basking, may protect lizards from early diurnal predators.

Caveats

As in other field observational studies, we cannot discount the possibility that our presence affected the behavior of studied animals (Davis & Balfour 1992). In particular, the effect of revisiting the same transect during the longitudinal study and of possibly triggering escape behavior during diurnal surveys are issues worth investigating. Also, as alluded to above, it would be informative to rigorously assess differences in both sleep duration and time of waking in dark (e.g., under forest canopy) and lighter (e.g., open) areas, for example by testing for correlation of these variables with some summary measure of light intensity. Finally, for each component of this study, our searches took place over a narrow window of diel time. Although one would expect the day–night transition that we studied to be most informative for issues of sleep duration and retiring and waking behavior, surveying over a continous 24-hour period would be complementarily useful.

Summary

Our study establishes a nighttime period of perch fidelity and nearly immobile sleep for 12 to 13 hours in our study anoles, from sundown to sunup, with narrow windows of diel transition when waking and retiring occur, and a brief period (< 1 hour) of inconspicuousness following waking. Our results were portended by other behavioral studies of anoles not focused on diel (i.e. sleep/wake) transitions. In particular, Clark & Gillingham (1990) noted overnight site fidelity in anoles, several authors have recorded sleeping posture and substrate in anoles (see references throughout this paper), and Rand (1967) described the behavior of *Anolis lineatopus* leaving exposed sleeping sites in the morning for the vegetative interior for some time before emerging to bask. We suspect that some of our results, such as overnight site fidelity and sleeping on light perches, are general to most anoles and many other tropical arboreal lizards. Although we note that we have observed other species of anole sleeping in leaf litter (e.g. *A. tropidonotus*), on rocks or logs (e.g., *A. aquaticus, A. notopholis*), or, rarely, under rocks or logs (*A. shrevei)* or ensconced in hanging moss (*A. quercorum*; we note that we have observed over 200 species of anole that appear to sleep almost exclusively on vegetation). Our other results, such as the brief periods of diel transition and the window of inconspicuousness after waking, may be more species or assemblage-specific.

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References

Allison, T. & D. V. Cicchetti (1976): Sleep in mammals: ecological and constitutional correlates. – Science, **194**(4266): 732–734.

Amadi, N. K., R. Belema, H. Obodo Chukwu, D. Dendi, A. Chidinma, R. Meek & L. Luiselli (2020): Life in the suburbs: artificial heat source selection for nocturnal thermoregulation in a diurnally active tropical lizard. – Web Ecology, **20**: 161–172.

Amlaner, C. J. & D. J. McFarland (1981): Sleep in the Herring Gull (*Larus argentatus*). – Animal Behaviour, **29**: 551–556.

Amlaner, C. J. & N. J. Ball (1983): A synthesis of sleep in wild birds. – Behaviour, **87**: 85–119.

Bors, M., N. P. Mohanty & P. Gowri Shankar (2020): Antipredatory sleep strategies are conserved in the agamid lizard *Monilesaurus rouxii*. – Behavioral Ecology and Sociobiology, **74**: 121.

Cabrera-Guzmán, E. & V. Hugo Reynoso (2010): Use of sleeping perches by the lizard *Anolis uniformis* (Squamata: Polychrotidae) in the fragmented tropical rainforest at Los Tuxtlas, Mexico. – Revista Mexicana de Biodiversidad, **81**, no. 3.

Campbell, S. & I. Tobler (1984): Animal sleep: a review of sleep duration across phylogeny. – Neuroscience and Biobehavioral Reviews, **8**: 269–300.

Christian, K. A., C. R. Tracy & W. P. Porter (1984): Physiological and ecological consequences of sleeping-site selection by the Galapagos Land Iguana (*Conolophus pallidus*). – Ecology, **65**: 752–758.

Clark, D. L. & J. C. Gillingham (1990): Sleep-site fidelity in two Puerto Rican lizards. – Animal Behaviour, **39**: 1138–1148.

Collette, B. B. (1961): Correlations between ecology and morphology in the Anoline Lizards from Havana, Cuba and Southern Florida. – Bulletin of the Museum of Comparative Zoology, **125(5)**: 135–162.

Davis, H. & D. Balfour (1992): The inevitable bond: examining scientist-animal interactions. – Cambridge University Press, New York.

Degenhardt, W. G., C. W. Painter & A. H. Price (1996): Amphibians and Reptiles of New Mexico. – University of New Mexico Press.

Elgar, M. A., M. D. Pagel & P. H. Harvey (1988): Sleep in mammals. – Animal Behaviour, **36**: 1407–1419.

Flannigan Jr., W. F. (1973): Sleep and wakefulness in the Iguanid lizards, *Ctenosaura pectinata* and *Iguana iguana*. – Brain, Behavior & Evolution, **8**: 401–436.

Goto, M. M. & M. A. Osborne (1989): Nocturnal microhabitats of two Puerto Rican grass lizards, *Anolis pulchellus* and *Anolis krugi*. – Journal of Herpetology, **23**: 79–81.

Huey, R. B., C. R. Peterson, S. J. Arnold & W. P. Porter (1989): Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. – Ecology, **70**: 931–944.

Huntley, A., M. Donnelly & H. Cohen (1977): Sleep in the desert iguana, *Dipsosaurus dorsalis*. – Sleep Research, **6:** 143.

Ikeuchi, I., M. Hasegawa & A. Mori (2012): Characteristics of sleeping sites and timing of departure from them in a Madagascan diurnal gecko, *Lygodactylus tolampyae*. – Current Herpetology, **31**: 107–116.

Kattan, G. (1984): Sleeping perch selection in the lizard *Anolis ventrimaculatus*. – Biotropica, **16**: 328–329.

Libourel, P. A. & A. Herrel (2016): Sleep in amphibians and reptiles: a review and a preliminary analysis of evolutionary patterns. – Biological Review, **91**: 833–866.

Meddis, R. (1975): On the function of sleep. – Animal Behaviour, **23**: 676–691.

Mohanty, N., M. Joshi & M. Thaker (2021): Urban lizards use sleep sites that mirror the structural, thermal, and light properties of natural sites. – Behavioral Ecology and Sociobiology, **75**: 166.

Mohanty, N. P., C. Wagener, A. Herrel & M. Thaker (2022): The ecology of sleep in non-avian reptiles. – Biological Reviews, **97:** 505–526.

Pereira, J. J., E. P. Lopes, M. A. Carretero & R. Vasconcelos (2019): Insular geckos provide experimental evidence on refuge selection priorities by ectotherms. – Behavioural Processes, **164**: 260–267.

Pianka, E. R. & L. J. Vitt (2003): Lizards: windows to the evolution of diversity. – University of California Press.

Pieron, H. (1913): Le probleme physiologique du sommeil. – Masson, Paris: 1–520.

Rand, A. S. (1967): Ecology and social organization in the Iguanid lizard *Anolis lineatopus*. – Proceedings of the United States National Museum, **122**: 1–79.

Rattenborg, N. C. & D. Martinez-Gonzalez (2015): Avian versus mammalian sleep: the fruits of comparing apples and oranges. – Current Sleep Medicine Reports, **1**: 55–63.

Romo, R., C. Cepeda & M. Velasco (1978): Behavioral and electrophysiological patterns of wakefulness-sleep states in the lizard *Phrynosoma regali*. – Boletin de Estudios Medicos y Biologicos (Mexico), **30**: 13–18.

Schwartz, A. & R. W. Henderson (1991): Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history. – University of Florida Press.

Shew, J. J., S. C. Larimer, R. Powell & J. S. Parmerlee Jr. (2002): Sleeping patterns and sleep-site fidelity of *Anolis gingivinus* on Anguilla. – Caribbean Journal of Science, **38**: 136–138.

Shine, R. (1987): Food habits and reproductive biology of Australian snakes of the genus *Hemiaspis* (Elapidae). – Journal of Herpetology, **21**: 71–74.

Siegel, J. (2005): Clues to the functions of mammalian sleep. – Nature, **437**: 1264–1271.

Singhal, S., M. A. Johnson & J. T. Ladner (2007). The behavioral ecology of sleep: natural sleeping site choice in three *Anolis* lizard species. – Behaviour, **144**: 1033–1052.

Steinmeyer, C., H. Schielzeth, J. C. Mueller & B. Kempenaers (2010): Variation in sleep behaviour in free-living blue tits, *Cyanistes caeruleus*: effects of sex, age and environment. – Animal Behaviour, **80**: 853–864.

Storks, L. & M. Leal (2020): Sleeping behavior of the secretive Puerto Rican twig anole, *Anolis occultu*s. – Caribbean Journal of Science, **50**: 178–187.

Vitt, L. J., T. C. S. Avila-Pires, P. Zani, S. S. Sartorius & M. C. Espósito (2003a). Life above ground: ecology of *Anolis fuscoauratus* in the Amazon rain forest, and comparisons with its nearest relatives. – Canadian Journal of Zoology, **81**: 142–156.

Vitt, L. J., T. C. S. Avila-Pires, M. C. Espósito, S. S. Sartorius & P. A. Zani (2003b): Sharing Amazonian rain-forest trees: ecology of *Anolis punctatus* and *Anolis transversalis* (Squamata: Polychrotidae). – Journal of Herpetology, **37**: 276–285.

Whewell, W. (1840): The philosophy of the inductive sciences, founded upon their history. – Scientific and Medical Knowledge Production, **1796–1918**: 21–25.