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The behavioral ecology of sleep: Natural sleeping site choice in three *Anolis* lizard species

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Summary

Where animals sleep may be an important component of their behavioral ecology, as sleeping renders animals immobile and hypothetically vulnerable for long periods. Yet, sleep is rarely studied outside of the laboratory. To investigate factors that influence natural sleeping behavior, we examined sleeping locations of three sympatric species of territorial *Anolis* lizards (*Anolis lineatopus*, *A. grahami* and *A. valencienni*) that have evolved adaptations to different microhabitats. Results indicate that sleeping perch differences among these species are consistent with their diurnal specializations, and sleeping perches are generally higher, narrower, and more horizontal than diurnal perches. We find only limited evidence for sleeping site fidelity; although individuals of one species have apparent sleeping areas within their home ranges, few lizards repeatedly sleep on perches within 0.5 m of previous sleep perches. In a closer examination of the sleeping sites of *A. lineatopus*, we find that male nocturnal ranges are more dispersed from conspecific males than their diurnal ranges, and they typically sleep near their territory boundaries. We conclude that while *Anolis* sleeping site choice is strongly influenced by diurnal behavior (including territorial defense and microhabitat choice), differential diurnal and nocturnal microhabitat use may result from differing pressures during day and night.

Keywords: *Anolis* lizards, microhabitat use, perch choice, sleep, territoriality.

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Introduction

Most animals spend up to half of each day (or more) in the behavioral state of sleep, yet sleep remains an understudied aspect of behavioral ecology (Lima et al., 2005). Despite the importance of sleep, the diurnal activities of animals receive much more attention, and our current understanding of sleeping behavior is largely based on laboratory studies of sleep physiology (e.g., Mathews & Amlaner, 2000; Lima et al., 2005) and anecdotal observations of sleeping animals in natural habitats (e.g., Rand, 1967). While valuable, these studies lack the ecological context necessary to understand the 'real world' implications of sleeping behavior (but see Christian et al., 1984; Clark & Gillingham, 1990; Anderson, 1998). With the notable exception of primates (reviewed in Anderson, 1998), remarkably little is known about natural sleeping behavior in most taxa.

The selection of sleeping sites can have critical consequences for individual fitness, as these sites may provide access to necessary diurnal resources and/or protection from predation or natural elements. In particular, the risk of predation during sleep has been suggested as an important, if not the most important, factor in sleeping site choice (e.g., Anderson, 1998; Ramakrishnan & Coss, 2001; Lima et al., 2005). Hamilton III (1982) suggested that animals prefer to sleep in locations that are either less vulnerable to predation (e.g., denser vegetation) or that are more sensitive to predators approaching (e.g., flimsier perches). For example, green-winged teals (*Anas crecca crecca*) had less restful sleep when sleeping in open, vulnerable areas than in more protected areas unless they slept in groups (Gauthier-Clearc et al., 1998). Other species, such as the Bermuda chub (Eristhee & Oxenford, 2001) and the golden-handed tamarin (Day & Elwood, 1999), used sleeping sites that were supportive and well-sheltered from predation attempts. Some animals go as far as building protective shelters for sleeping, including many parrotfish species that surround themselves at night with a transparent mucus cocoon. This cocoon likely serves as an antipredator device both by reducing odors emanated from the fish and warning the fish of approaching predators (Winn, 1955; Winn & Bardach, 1959; Shephard, 1994). Despite the likely importance of predation avoidance in sleeping site selection, there is almost no available information on quantified nocturnal predation risk in natural areas.

Other sleeping site criteria may also affect the fitness of individuals. First, sleeping site proximity to feeding or basking sites may be important to ensure easy access to these sites upon waking, as shown for several lizard species (Christian et al., 1984; Kattan, 1984; Clark & Gillingham, 1990). Second, because sleep has important restorative functions (e.g., Meddis, 1975; Anderson, 1998), some researchers have pinpointed expected quality of sleep as an important factor in sleeping site choice (Lima et al., 2005). For example, many primates sleep in habitats that are sheltered from weather disturbances (reviewed in Anderson, 1998) or that provide preferred thermal conditions (Bakken, 1992). Finally, in spite of the other factors that determine where animals choose to sleep, sleeping site location may be constrained by site availability or where other conspecifics sleep (e.g., degree of crowding; Lima et al., 2005).

Caribbean lizards in the genus *Anolis* (i.e., anoles) provide an excellent opportunity for studies of sleeping behavior. Anoles, and reptiles in general, have distinct periods of sleep as determined by behavioral, neurological, and electrophysiological evidence (Meddis, 1975; Clark & Gillingham, 1990; Mathews & Amlaner, 2000). Anoles are among the most populous vertebrates on most Caribbean islands, and they can easily be observed sleeping in their natural environments. In particular, these diurnal lizards typically sleep in exposed positions, perching on leaves or twigs near the ends of branches. Also, because anoles are territorial, they can repeatedly be located in the same areas during both diurnal and nocturnal observations.

In this study, we compare diurnal and nocturnal microhabitat use in three sympatric species of Jamaican *Anolis* lizards: *A. lineatopus*, *A. grahami* and *A. valencienni*. During the day, these species use different arboreal microhabitats and display morphological, ecological, and behavioral adaptations to these microhabitats (Williams, 1983; Losos, 1990). *Anolis lineatopus* is a medium-sized brownish lizard (average male SVL $\approx$ 53 mm) that primarily occurs on tree trunks and the ground, *A. grahami* is a medium-sized bluish-green species (average male SVL $\approx$ 54 mm) that typically perches on tree trunks and large branches several meters above the ground, and *A. valencienni* is a medium to large-bodied gray lizard (average male SVL $\approx$ 64 mm) that crawls along narrow twigs and branches in the canopy. Here, we test the hypothesis that the three species use different sleeping habitats, and that these differences correspond to the species' different diurnal microhabitat specializations (Hypothesis 1). Also, because diurnal and nocturnal pressures may differ (as lizard predators differ between day and night, and territory defense and food procurement structure daytime, but not likely nighttime, habitat use) we predict that anoles will sleep in different microhabitats than those they use during the day (Hypothesis 2).

We also examine the hypothesis that anoles exhibit sleeping site fidelity (Hypothesis 3). Several previous studies suggest that lizards may display such fidelity (*Anolis* lizards: Clark & Gillingham, 1990; Shew et al., 2002; *Sceloporus undulatus*, Kennedy, 1959; *Conolophus pallidus*, Christian et al., 1984) because high quality sleeping sites (e.g., those that provide maximum security during sleep; Clark & Gillingham, 1990) within an individual's range may be rare. Therefore, as a measure of whether anoles repeatedly use sleeping perches in close proximity to their previous sleeping perches, we test the prediction that individuals' sleeping ranges are significantly smaller than their diurnal territories.

Finally, because such little work has examined natural sleeping site location, we perform a more detailed investigation of the sleeping sites of one species, *Anolis lineatopus*. In particular, we examine the spatial arrangement of sleeping sites as compared to the arrangement of their diurnal territories.

Materials and methods

Study site and focal species

We observed the diurnal and nocturnal habitat use of three species of *Anolis* lizards during June-August 2005 in the coastal forest surrounding the Discovery Bay Marine Laboratory (18.4°N, 77.4°W) in Discovery Bay, St. Ann, Jamaica. Our study site was dominated by the mangrove forest community and the limestone karst terrain typical of the northern coast of Jamaica. We established three $\sim$500 m^2 plots with similar habitat characteristics (i.e., the plots had similar canopy heights, sun exposure, and available perch diameters and inclinations; also see Results), in which we captured, sexed, and measured the snout-vent length (SVL) of all adult lizards of the study species: *Anolis lineatopus*, the Jamaican gray anole, *A. grahami*, the Jamaican turquoise anole, and *A. valencienni*, the Jamaican twig anole. To identify lizards for future observations, we sewed unique bead tags into the proximal region of the tail (Fisher & Muth, 1989) or attached queen bee marking tags to the dorsum (Johnson, 2005). All three species co-occurred in our study plots, but at different densities. We captured a total of 175 *A. lineatopus* (0.087 adults/m^2), 133 *A. grahami* (0.084 adults/m^2) and 87 *A. valencienni* (0.013 adults/m^2).

Perch use

In each plot, we observed diurnal lizard perch use each day (0700-1830 h) during a two week period and sleeping perch use on five nights (2200-0100 h) during the same period. We did not collect perch use data during inclement weather, as lizards may dramatically adjust their perch use during those times (Losos, 1990; Hertz et al., 1993). To quantify perch use, we measured perch characteristics where we initially sighted each lizard. Specifically, we measured perch height, diameter and angle of perch inclination (0-90°, where 0° is perpendicular to the ground), and we recorded the substrate of the perch (e.g., branch, leaf, rock). At night, we marked sleeping perches with flagging tape but did not measure them until the following day to minimize disturbances to the sleeping lizards. We averaged perch measurements for diurnal and sleeping perches for each lizard and square-root transformed perch height and diameter to meet assumptions of normality.

To examine perch availability and to determine if the three plots were similar in habitat characteristics, we measured available perches along two transects intersecting the study plots (following Johnson et al., 2006). To this end, at 1-m intervals along the 25-m transects, we measured the diameter and inclination of two haphazardly chosen perches at each of four heights (0.5, 1.0, 2.0 and 3.0 m). These heights encompass the typical heights of the focal species at this site (Figure 1a). A multivariate analysis of variance (MANOVA) comparing the perch characteristics of these two transects revealed no significant differences ($p > 0.15$) among plots, so we pooled data from all plots in subsequent analyses. To determine if lizards chose diurnal and sleeping perch sites at random in the forest, we performed MANOVAs comparing the diameter and inclination of 'available' perches with 'utilized' perches (examined separately for diurnally and nocturnally used perches).

To determine differences in perch use characteristics among the three species, between males and females, and between night and day, we performed a multivariate analysis of covariance (MANCOVA) with SVL as the covariate. In this analysis, perch height, diameter, and inclination were the dependent variables and species, time (night vs. day) and sex were the independent variables. We used follow-up ANCOVAs and Tukey's HSD post-hoc tests to characterize significant differences. Finally, we conducted a chi-square test to examine whether substrate use differed between day and night.

Nocturnal vs. diurnal home range size

To determine whether lizards choose sleeping sites from a limited portion of their diurnal home range, during our daily and nightly observations, we determined each lizard's two-dimensional position within the plot by measuring the distance and angle of its perch to predetermined reference points and converting these data into Cartesian coordinates. Because we rarely repeatedly located *A. grahami* at night, we included only *A. lineatopus* and *A. valencienni* in the home range analysis. Although we measured 20 or more diurnal locations for many of the lizards in this study, we measured a maximum of 5 nocturnal locations per lizard. Therefore, to ensure that differences between diurnal and nocturnal home range areas were not an artifact of the number of points used to define the ranges (Schoener, 1981), we only used diurnal data collected on the same day as nocturnal data. For example, if a lizard was located on four nights, we estimated its diurnal range using diurnal locations from the same four days. We excluded lizards with fewer than three nocturnal locations. We estimated the diurnal and nocturnal areas used by each lizard with Minimum Convex Polygons (MCP; Rose, 1982) using Calhome (Kie et al., 1996). While 3-5 points are not sufficient to determine the general space use of animals, we use this approach as a measure of the difference between nocturnal and diurnal space use in a short time period and not to estimate the amount of space required for all aspects of an individual's life. Because sample sizes were small and diurnal and nocturnal range sizes were matched by individual, we used Wilcoxon's signed-ranks test to compare diurnal and nocturnal range sizes within species. To compare range sizes between the two species, we used a Mann-Whitney U-test.

To determine the extent to which lizards return to the same sleeping site on multiple nights, for each sleeping lizard located on more than one night, we calculated the distance between the first night's sleeping site and all subsequent sleeping sites. We then calculated an average for each individual and compared these distances between sexes within each species, and between the two species using Mann-Whitney U-tests.

Spatial arrangement of sleeping sites in A. lineatopus

To determine whether the spatial distribution of *A. lineatopus* sleeping areas differed from the distribution of diurnal territories, we calculated the centroid of both diurnal and nocturnal MCPs, defining MCPs as described above. We then determined the distance among centroids for these ranges and calculated the average distance of each lizard's range from all conspecific individuals in its plot, with diurnal and nocturnal ranges considered separately. We tested for differences between average diurnal and nocturnal distances using Wilcoxon's signed-ranks test, with data paired by individual.

To determine whether *A. lineatopus* sleeping sites were located within their diurnal territories, we used all diurnal location data (4-20 sightings per lizard) to estimate 95% MCPs and adaptive density kernels (ADK; Seaman & Powell, 1996) using Calhome. ADKs appear to overestimate an individual's peripheral use of its range (Seaman & Powell, 1996; Powell, 2000); thus our estimate of the number of lizards sleeping outside of their home ranges using this approach was more conservative than the MCP approach. We used ArcGIS 9 to measure the shortest distance from sleeping locations to the territory edge. We also measured the distance from the center to the territory edge with the line that passed through the sleep location. The ratio of these two distances (distance of sleeping location to territory edge/radius of territory) provided an index of the spread of sleeping locations standardized by the relative size of the territory. If a sleep location was close to the territory edge, the ratio for this location was a value close to 0. We assigned negative values to locations outside of the territory and positive values to locations inside the territory. To determine whether the ratio values were influenced by the number of points used to define the home range, we calculated Pearson correlation coefficients.

Results

Perch use

Lizards' sleeping perch use, as measured by perch diameter and inclination, reflects a non-random subset of available perches. The average sleeping ($N = 157$) and diurnal perches ($N = 246$) of *Anolis* lizards are wider and more vertically oriented than randomly available perches (MANOVA: sleeping $F_{2,520} = 50.73$, $p < 0.0001$; diurnal $F_{2,609} = 39.95$, $p < 0.0001$).

We consider differences in perch use characteristics among the three species, between the sexes, and between night and day in a MANCOVA (Table 1). All significant ($p < 0.05$) follow-up ANCOVA results are indicated

Table 1. Results from MANCOVA examining variation in perch characteristics (height, diameter, inclination). In this analysis, we compared perches used by males vs. females (sex), diurnal vs. sleeping perches (time) and perches used by the three study species (species), and the interactions among these factors, with SVL (size) as the covariate. For significant main effects, we conducted follow-up ANCOVAs. Bold values indicate significant differences.

	Wilks' λ	df	*F*	*p*
Size	0.945	3, 387	7.48	**<0.001**
Height		1, 389	18.74	**<0.001**
Diameter		1, 389	1.90	0.169
Inclination		1, 389	0.35	0.557
Sex	0.998	3, 387	0.29	0.883
Time	0.750	3, 387	43.01	**<0.001**
Height		1, 389	22.30	**<0.001**
Diameter		1, 389	55.82	**<0.001**
Inclination		1, 389	44.39	**<0.001**
Species	0.692	6, 774	26.05	**<0.001**
Height		2, 389	60.20	**<0.001**
Diameter		2, 389	21.45	**<0.001**
Inclination		2, 389	1.10	0.334
Sex × Time	0.939	3, 387	8.37	**<0.001**
Height		1, 389	22.94	**<0.001**
Diameter		1, 389	2.64	0.105
Inclination		1, 389	0.001	0.981
Sex × Species	0.957	6, 774	3.27	**0.004**
Height		2, 389	3.00	0.051
Diameter		2, 389	2.93	0.055
Inclination		2, 389	3.62	**0.028**
Time × Species	0.913	6, 774	6.03	**<0.001**
Height		2, 389	10.37	**<0.001**
Diameter		2, 389	3.33	**0.037**
Inclination		2, 389	2.84	0.060
Sex × Time × Species	0.982	6, 774	1.21	0.300

in Figure 1. We did not apply Bonferroni multiple-test corrections to these results because in our 27 pair-wise comparisons, at a nominal *P* value of 0.05 we might expect 1-2 false significant results to occur by chance; however, when using the Bonferroni method, we found that 6 comparisons became non-significant. Following Johnson et al. (in press), we believe the benefit of protection from Type-I error is surpassed by the cost in reduced statistical

Table 2. p values from ANCOVAs comparing day and night perch characteristics within a sex within a species, and ANCOVAs comparing perch characteristics between the sexes within a species. The covariate in all analyses was SVL. NS indicates p values > 0.05.

Comparison	Height	Diameter	Inclination
A. lineatopus			
male, day-night	<0.001	<0.001	<0.001
female, day-night	<0.001	<0.001	<0.001
male-female	<0.001	NS	NS
A. grahami			
male, day-night	NS	NS	0.040
female, day-night	0.016	0.017	0.017
male-female	0.035	NS	NS
A. valencienni			
male, day-night	NS	0.007	NS
female, day-night	0.001	<0.001	NS
male-female	NS	NS	NS

power resulting from multiple-test correction (Moran, 2003). We provide the p values from our pair-wise comparisons in Table 2.

Univariate ANCOVAs following the significant time (day vs. night) effect indicate that lizards' sleeping perches are significantly higher, narrower, and more horizontal than their diurnal perches (Table 1 and Figure 1). Exceptions to this general pattern are male *A. grahami* and *A. valencienni*, which perch slightly but non-significantly lower at night than during the day (Figure 1a). The significant species effect and univariate follow-up tests indicate that the three species use significantly different perches than one another. While much previous work has established the differences in diurnal perches among these species (e.g., Schoener & Schoener, 1971; Williams, 1983; Losos, 1990), Tukey's HSD post-hoc tests show that these three species partition sleeping sites to as great an extent as they partition daytime microhabitat use. For example, during the day and at night, *A. valencienni* uses the highest perches, *A. grahami* uses perches at intermediate heights and *A. lineatopus* uses the lowest perches (Figure 1a). Further, *A. valencienni*, a species typically found on small twigs and branches during the day, uses sleeping perches significantly narrower than that of both *A. grahami* and *A. lineatopus* (species occurring on tree trunks; Figure 1b) and significantly more vertical

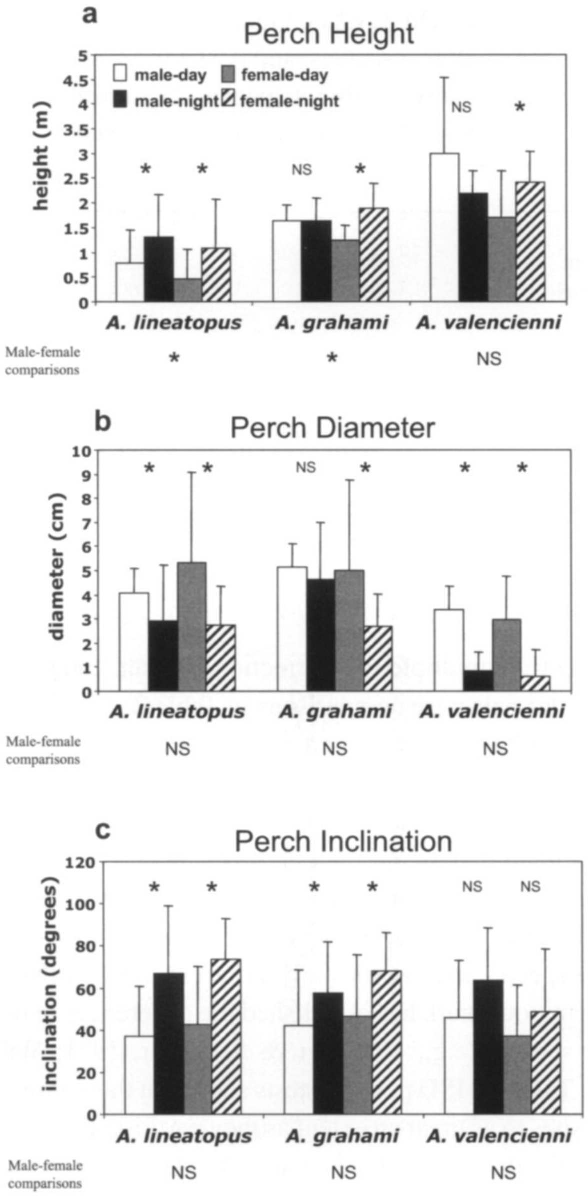

Figure 1. Mean + 1 SE nocturnal and diurnal perch height (a), diameter (b) and inclination (c) of male and female *Anolis lineatopus*, *A. grahami* and *A. valencienni*. Significant ($p < 0.05$) day-night comparisons for each sex within each species are denoted with an asterisk above the bars, and significant male-female comparisons within each species are denoted with an asterisk below the graphs. NS indicates non-signficance.

than that of *A. lineatopus* (Figure 1c). We did not, however, find a significant sex main effect.

In addition to these main effects, we also find significant sex × time, sex × species, and time × species interactions, indicating that the three species and the sexes do not display consistent differences between daytime and sleeping perches. In particular, *A. valencienni*'s sleeping perches narrow significantly more at night than *A. grahami* or *A. lineatopus* (Figure 1b). Additionally, males and females differ in their degree of differences between diurnal and sleeping perch height, with female lizards increasing their sleeping perch height much more relative to daytime perches than male lizards (Figure 1a).

Further, substrate use at night differs dramatically from daytime use; the chi-square test comparing day and night substrate use is significant ($\chi^2_3 = 352.06$, $p < 0.001$). In particular, *A. lineatopus* and *A. grahami* sleep almost exclusively on branches and leaves at night, whereas they rarely perch on leaves during the day (Figure 2). However, the substrate use of *A. valencienni*

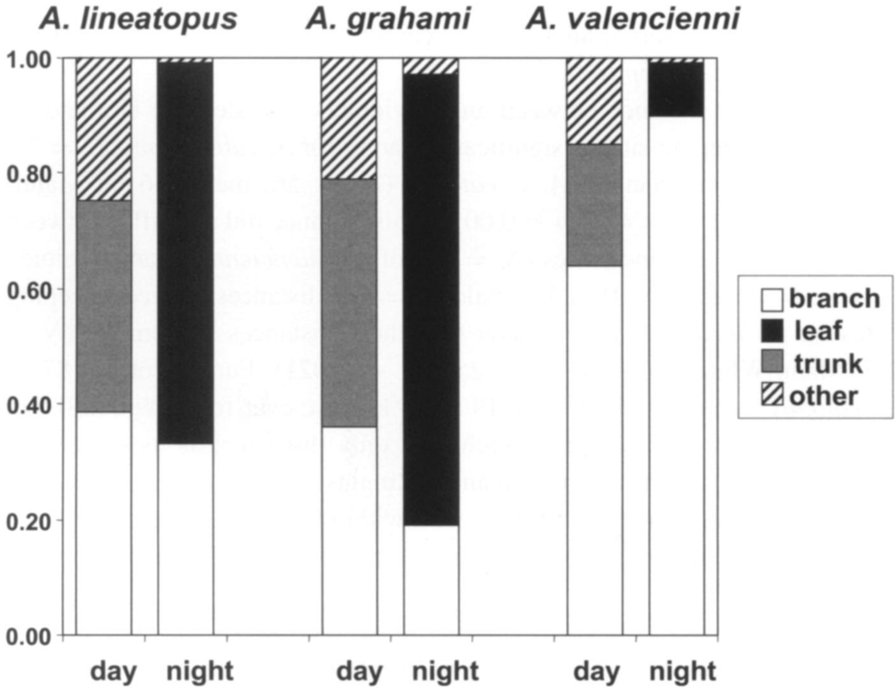

Figure 2. Perch substrate for species at day and night. 'Other' consists of ground and bromeliad perches.

does not differ as dramatically between day and night — they typically perch on branches and twigs during both periods (Figure 2). Here, 'other' perches consist of ground and bromeliad perches.

Nocturnal vs. diurnal home range size

The average diurnal home range (as estimated using 3-5 diurnal sightings of each lizard; see Materials and methods) for *A. lineatopus* ($N = 25$) is 4.7 m^2 and their average nocturnal range is 0.99 m^2, or 21% of the diurnal home range size. The average diurnal home range for *A. valencienni* ($N = 16$) is 48.2 m^2 and their average nocturnal range is 37.2 m^2, or 77% of the diurnal home range. Although both species show a decrease in nocturnal range area with respect to diurnal area, the difference in diurnal and nocturnal ranges is statistically significant only for *A. lineatopus* (Wilcoxon's signed-rank test: *A. lineatopus*: $Z = -2.03$, one-tailed $p = 0.021$, *A. valencienni*: $Z = -0.60$, one-tailed $p = 0.273$). A Mann-Whitney U-test comparing nocturnal areas for *A. lineatopus* and *A. valencienni* shows that *A. valencienni*'s average nocturnal area is significantly larger ($U = 12$, $p < 0.001$) than that of *A. lineatopus*.

The average distance between an individual's first sleeping site and all subsequent sleeping sites is significantly larger for *A. valencienni* ($N = 33$, mean $= 7.4$ m) than for *A. lineatopus* ($N = 56$, mean 3.6 m; Mann-Whitney U-test: $U = 425$, $p < 0.001$). This distance did not differ between females ($N = 22$) and males ($N = 11$) of *A. valencienni* (Mann-Whitney U-test: $U = 117$, $p > 0.1$), but male ($N = 31$) distances between sleeping sites for *A. lineatopus* were greater than those distances for females ($N = 25$; Mann-Whitney U-test: $U = 255$, $p < 0.021$). Further, of the 87 *A. lineatopus* located at night, only 19 (21.8%) were ever found within 0.5 m of a previously used sleeping perch, and only three lizards used sleeping perches within 0.5 m on more than two nights. Of the 41 *A. valencienni* located at night, four (9.8%) were found within 0.5 m of a previously used sleeping perch, and none used sleeping perches within 0.5 m on more than two nights.

Spatial arrangement of sleep sites in A. lineatopus

The average distance of the centroid of *A. lineatopus* ($N = 25$) diurnal ranges from other diurnal ranges in the same plot is 11.2 m, and the average nocturnal distance is 11.8 m. Male sleeping ranges are marginally significantly more distantly distributed than their diurnal ranges (Wilcoxon's signed-ranks test: $N = 14$, $Z = -1.852$, $p = 0.06$), although female sleeping ranges are not more distantly distributed than their diurnal ranges (Wilcoxon's signed ranks test: $N = 11$, $Z = -0.800$, $p = 0.42$).

We use both minimum convex polygons (MCP) and adaptive kernels to determine whether *A. lineatopus* ($N = 23$) choose non-random sleeping sites in relation to their diurnal territories. Using MCPs, the distance of sleeping site from territory edge/distance of center to territory edge ratio is significantly correlated with the number of diurnal points used to define the home range ($r = 0.42$, $p = 0.049$), indicating that lizards' sleeping sites are more likely to be located within diurnal territories when territories are defined by a greater number of sightings per lizard. Adaptive kernels are less sensitive to the number of points used to define a territory, and we do not see a significant correlation of ratio value with number of diurnal points using this method ($r = 0.24$, $p = 0.25$). Therefore, we only further examine the data using adaptive kernels. Using this approach, the average ratio value is -0.1 and the median ratio value is 0.1. Very few lizards slept near the center of their diurnal territory, and most lizards sleep near the periphery of the territory.

Discussion

Perch use

This study shows that sleeping perch use in Jamaican *Anolis* lizards is strongly related to their morphological habitat specializations but suggests that different selective pressures acting at day and night result in different diurnal and sleeping perch use. These results indicate that ecological differences among these species influence sleep site selection.

The sleeping perches of the three species reflect the microhabitat specialization seen during the day (Hypothesis 1). Caribbean *Anolis* lizards display morphological specializations to particular microhabitats (e.g., Losos, 1990); for example, lizards that occur on broad surfaces (such as tree trunks) in the daytime have longer legs. Here, we find that these diurnal specializations strongly influence sleeping perch use as well, as species that use higher perches in the day use higher sleeping perches, and those that occur on broader perches during the day use broader sleeping perches (Figure 1). The morphological differences among these species allow them to maximize their locomotor speed and/or surefootedness in different microhabitats (Irschick & Losos, 1998, 1999); therefore, using different sleeping perches that correspond to their morphological specializations may allow the animals to efficiently locomote upon waking or in case of an approaching predator. The generality of this pattern of interspecific differences in sleeping site choice is yet to be determined. Few studies have investigated the sleeping behavior of multiple species, although Heymann (1995) also saw nocturnal niche specialization in two tamarin species, as did Goto & Osborne (1989) in two Puerto Rican *Anolis* species that occupy distinct diurnal microhabitats.

We further find that all three species exhibit differences in diurnal and sleeping perch use (Hypothesis 2). In particular, substrate use changes dramatically, as both *A. lineatopus* and *A. grahami* move from perching on trunks and branches during the day to using mostly leaves at night. However, *A. valencienni* was found perching almost exclusively on branches at both times of day, but uses narrower branches for sleeping perches. These changes in substrate are reflected in the quantitative changes in perch dimensions, as sleeping perches tend to be narrower and on less stable substrates than diurnal perches. Further, they are more exposed, as *A. lineatopus* and *A. grahami* are typically found sleeping on the outer surface of a leaf. Lima and his colleagues (2005) suggested that a trade-off exists regarding sleeping site exposure, as sites that provide protection from predation often prevent the animal from obtaining cues about its immediate surroundings. However, exposed perches better enable the organism to detect an approaching predator as they are more visually and physically sensitive to movement. When an *Anolis* sleeping perch is disturbed, the animal typically drops immediately to the ground and flees. Although predators on anoles are not common in island ecosystems such as Jamaica (Andrews, 1979; Lister, 1981; Greene, 1988), predation can remain an important factor even when rare due to its strong selective pressure (McLaughlin & Roughgarden, 1989), and the risk of predation is likely an important factor in determining sleeping perches in these lizards. In fact, during the course of this study, we observed a nocturnal predation event by the Jamaican boa (*Epicrates subflavus*) on an *A. valencienni* adult.

Several researchers studying sleep in other *Anolis* species (Kattan, 1984; Chandler & Tolson, 1990) have found significant differences in male and female sleeping perch heights and diameters. These researchers hypothesized that males perch differently from females so that they will be in optimal positions for territorial defense upon waking. In this study, we fail to find any significant main effect differences in male and female perch use, despite significant differences in diurnal perch use. During the day, differences in perch height (which is highly correlated with perch diameter) between males and females of the same species may exist to reduce food competition between the sexes (particularly for the highly sexually size dimorphic *A. lineatopus* and *A. grahami*; Schoener, 1967, 1968; but see Stamps et al., 1997) or for optimal territorial defense (Scott et al., 1976). At night, these pressures would presumably be relaxed, reducing the pressure for the two sexes to use different perches.

Nocturnal vs. diurnal home range size

We tested the hypothesis that *Anolis* lizards repeatedly use sleeping perches in close proximity to their previous sleeping perches (Hypothesis 3), a concept related to, but different from classic sleeping site fidelity in which an animal repeatedly uses the same location for sleeping. Shew et al. (2002) hypothesized that fidelity to a sleeping site could reflect a paucity of adequately safe nighttime perches in the typical home range. Thus, organisms may be driven to sleep in similar sites nightly to ensure protection from predators and natural elements. Sleeping site fidelity has been shown in taxa as diverse as gibbons (Reichard, 1998), Bermuda chub (Eristhee & Oxenford, 2001), woolly mouse opossum (Moraes & Chiarello, 2005), ground squirrels (Michener, 2002) and anoles (Clark & Gillingham, 1990). Because *Anolis* are known to be territorial (Stamps, 1983), we consider fidelity to sleeping site in the context of the animals' diurnal territories. In particular, if an animal uses a significantly smaller area for sleeping than it does for its daytime activities, we conclude that fidelity to a sleeping area is displayed. We find that one of the two species examined, *A. lineatopus*, exhibits such fidelity, sleeping in a limited portion of their diurnal ranges. However, our study does not find levels of fidelity as high as Rand (1967), who describes *A. lineatopus* as sleeping on the same branch nightly. Further, our results show that *A. valencienni*, which has been characterized as having a relatively large home range for anoles (Hicks & Trivers, 1983), uses a larger range than *A. lineatopus* at night. It is possible that *A. valencienni*'s larger home range affords them a greater number of well-protected sleeping sites, or that their greater diurnal movement carries them too far to return to the same sleeping sites.

Spatial arrangement of sleep sites in A. lineatopus

Rand (1967) reported anecdotal observations that *A. lineatopus* appear to cluster at night. In contrast, our results show that these lizards are more dispersed at night than during the day. This result is only significant for male *A. lineatopus*, while females are equally dispersed during the day and at night. We suggest two mechanisms that may explain this pattern. First, lizards may cluster around food sources during the day, but they spread out at night when they are no longer feeding. However, if this were the case, we would have no reason to expect to see differences in male and female sleeping site dispersal. Second, in most *Anolis* species, males spend a greater portion of their day actively patrolling and defending their territory (Stamps, 1994; Nunez et al., 1997), so they may position themselves more closely to conspecifics in attempts to expand or prevent intrusions into their territories. Males may then be relatively more dispersed at night because the pressures to defend their territories are reduced.

We also quantified the location of sleeping sites with respect to their diurnal territories to determine whether lizards sleep within their diurnal ranges. There are several possibilities for the locations of the sleeping sites within the home ranges: the organisms could sleep (1) well within their territories, (2) near the territories' boundaries, (3) well outside their territories, or (4) in no overall pattern. Although substantial individual variation exists, the majority of *A. lineatopus* sleep near the boundaries of their home ranges.

We propose two possible explanations for these results. First, nighttime positions may be an artifact of positioning at the day's end. The few studies that have considered sleeping site location in relation to the organism's home range have concluded that sleeping sites are near areas extensively used during the day (e.g., Reichard, 1998, in gibbons; Mendes Pontes & Soares, 2005, in marmosets). However, these previous studies examined mammals with much larger home ranges than the lizards studied here. As *A. lineatopus* has a comparatively small home range in which it moves around daily, nighttime positioning is likely less bound to daytime positioning. Consistent with this idea, we see that these lizards seem to reserve specific areas of their home range for sleep. Second, lizards may sleep near their boundaries to be in an optimal position for territorial defense in the morning. Although one hypothesis we offer to explain the lack of sleep site clustering (see above) suggests that the pressure to defend a territory is relaxed at night, this does not preclude the possibility that lizards may position themselves to maximize defense in the morning. Indeed, Kattan (1984) observed that anoles engage in territorial displays upon waking, suggesting that nocturnal positions could have important consequences for territorial defense.

Conclusions

In sum, we show that *Anolis* sleeping site choice is strongly influenced by the species' diurnal behavior and their ecological and morphological specializations to different microhabitats. Although the three species display significant differences in sleeping site characteristics and fidelity to a sleeping area within the home range, there are also similarities among them in sleeping site selection. Each species examined here chose sleeping sites that were generally higher, narrower, and more horizontal than their diurnal perches, and differences in substrate use between day and night indicate that lizards generally prefer less structurally stable perches for sleeping. While differences among the species indicate the importance of ecological differences in determining sleeping sites, the similarities suggest that these species encounter similar nocturnal pressures in their varying microhabitats that have similar influences on the species' sleeping sites. Additional studies in the behavioral ecology of sleep in animals other than primates are needed to evaluate the generality of these findings.

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