

Sleep-site selection and fidelity in Grenadian Anoles

(Reptilia: Squamata: Polychrotidae)

Schlafplatzwahl und -treue bei Echsen der Gattung *Anolis* aus Grenada
(Reptilia: Squamata: Polychrotidae)

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KURZFASSUNG

Wir untersuchten Schlafplatzwahl und -treue bei zwei anscheinend syntopen Anolisarten, *Anolis aeneus* GRAY, 1840 und *A. richardii* DUMÉRIL & BIBRON, 1837 in Grenada, um die folgenden Vorhersagen zu prüfen: daß sich die zwei Arten in ihrer Schlafplatzwahl unterscheiden, daß sie Schlafplätze bevorzugen, die ihre Angreifbarkeit durch die Baumboa, *Corallus grenadensis* (BARBOUR, 1914), möglichst erschweren, und daß sie hohe Schlafplatztreue für sichere Plätze zeigen würden. Die Verschiedenheit der von beiden Arten benutzten Schlafplätze und die relativ hohe Nischüberschneidung legen nahe, daß sich diese Arten die vorhandenen Schlafplätze nicht untereinander teilen, wenigstens nicht an diesem Ort. Wir fanden keine Anzeichen dafür, daß diese Echsen Schlafplätze wählten oder Schlafverhaltensweisen zeigten, die ihre Angreifbarkeit durch *C. grenadensis* verringern würden. Auch fanden wir keine erhöhte Schlafplatztreue gegenüber vermutlich besonders sicheren Schlafplätzen. Die in dieser Gegend reiche Ausstattung mit den benötigten Requisiten macht eine gemeinsame Nutzung von Schlafplätzen offenbar nicht notwendig und die Häufigkeit der Eidechse verringert die individuelle Wahrscheinlichkeit, gefressen zu werden, so weit, daß der Selektionsdruck auf die Ausbildung von Feindabwehrverhalten schwach bis nicht vorhanden zu sein scheint.

ABSTRACT

We examined sleep-site selection and fidelity for two apparently syntopic anoles, *Anolis aeneus* GRAY, 1840 and *A. richardii* DUMÉRIL & BIBRON, 1837, in Grenada to test predictions that they would differ in sleep-site selection, that sleep-site selection would favor perches less vulnerable to predation by the arboreal treeboa, *Corallus grenadensis* (BARBOUR, 1914), and that individuals of both species would show high fidelity to sites safe from predation. The variety of perches used by both species and relatively high structural niche overlaps suggest that these two species do not partition available sleep sites, at least in these habitats. We found no evidence that indicated that lizards selected sleep sites or exhibited sleeping behaviors that minimized opportunities for predation by *C. grenadensis*, nor did we observe high levels of sleep-site fidelity for perches presumably less vulnerable to predation. The abundance of essential resources at this site apparently precludes a necessity for partitioning and the abundance of anoles sufficiently reduces the likelihood of predation on any individual such that selective pressures favoring the evolution of anti-predator behaviors are weak or non-existent.

KEY WORDS

Reptilia: Squamata: Polychrotidae: *Anolis aeneus*, *Anolis richardii*, Grenada, sleep-site selection, sleep-site fidelity, sleeping behavior

INTRODUCTION

Many studies have investigated the ecology of West Indian anoles (HENDERSON & POWELL 1999), but few have addressed sleeping behavior. Other than anecdotal information, such as notations of perch characteristics and waking behavior (summarized in SCHWARTZ & HENDERSON 1991), we are aware of only two quantitative studies that address this topic. CLARK & GILLINGHAM (1990) studied sleep behavior and sleep-site fidelity in *Anolis gundlachi* PETERS, 1876 and *A. cristatellus* DUMÉRIL & BIB-

RON, 1837 in two ecologically distinct areas on Puerto Rico, both of which were inhabited by nocturnal predators. SHEW et al. (2002) examined sleep-site fidelity and characteristics of *A. gingivinus* COPE, 1864 on Anguilla, an island inhabited by a single native *Anolis* species that is subjected to little or no nocturnal predation pressure. Neither study addressed the spatial distribution of sleep sites, nor did either relate site selection and use to habitat utilization by nocturnally active predators on anoles.

Anolis aeneus GRAY, 1840 and *Anolis richardii* DUMÉRIL & BIBRON, 1837 are endemic to the Grenada Bank, where they are the only native representatives of the genus. On Grenada, both species are virtually ubiquitous (GERMANO et al. 2003). SCHOENER & GORMAN (1968) noted that *A. richardii* was sometimes found to the nearly complete exclusion of *A. aeneus* in well-shaded forests, whereas *A. aeneus* was far more abundant in open sun-filled areas. These apparent differences in habitat preference presumably accounted for the significantly lower body temperatures in shade-loving *A. richardii*. Larger *A. richardii* also consumed larger prey. However, in areas of intermediate habitat conditions, where both species were abundant, they appear to be essentially synoptic (HARRIS et al. 2004).

From 8–21 June 2002, at Westerhall Estate, St. David Parish, Grenada, a site at which the arboreal boa, *Corallus grenadensis* (BARBOUR, 1914), an active nocturnal predator on sleeping anoles, is common (HENDERSON 2002), we examined sleep-site selection, fidelity to sleep sites, and spatial distribution of *A. aeneus* and *A. richardii* to test the following predictions:

P₁: Sleep-site characteristics will differ between the two species in order to partition available sleep sites and optimize distinctive ecological requirements.

P₂: Both species will exhibit sleep-site selection and sleeping behaviors that minimize predation by *Corallus grenadensis*.

P₃: Both species will demonstrate high levels of sleep-site fidelity for perches safe from predation.

MATERIALS AND METHODS

The study site was a 40-m transect located at Westerhall Estate (12°01'31"N, 61°42'26"W; elevation 41 m). The transect line followed an unpaved and infrequently used road in an area of abandoned mixed agriculture. The transect paralleled the side of a hill, creating a topographical high and low side (the "dry woodland" and "stream-side forest," respectively, of HARRIS et al. 2004). HENDERSON (2002) and references therein provided additional descriptive details and photographs of the general area. Both sides contained mature (> 20 m) and immature trees, although the somewhat less densely shaded high side also contained some areas of open canopy, mats of interwoven vines, and many shrubs, some of which were thorny. The low side was dominated by large mature trees, contained very few vines and thorny shrubs, and had a contiguous canopy in excess of 20 m. Canopies of the two sides were in contact at several locations at heights of 3–15 m within the study site. *Corallus grenadensis* was commonly encountered in the area. Snakes used perches ranging from 0.3–16.0 m above the ground and 1–20 mm in diameter (HENDERSON 2002). During a concurrent study (YORKS et al. 2004), treeboas were observed searching for prey primarily on branches below that on which they were perched and

two successful predation attempts on sleeping anoles were recorded. HENDERSON (2002) calculated a population density in this area of 16–25 snakes/ha.

During 53 person-hours at times ranging from 1940–2200 h, we attempted to find all sleeping anoles within 6 m on either side of the road. Because of the difficulty of seeing anoles at greater heights, at least some of which were screened by the leaves upon which they slept, our survey was largely restricted to lizards sleeping at heights of < 4 m (most *A. richardii* slept at heights of < 1 m and the average perch height for *A. aeneus* was < 1.5 m). We did, however, scan possible perches at greater heights when possible. When HARRIS et al. (2004) surveyed essentially the same area during the day, they found few anoles on perches exceeding 4 m (mostly adult *A. aeneus* on the low side of the transect). Although they were similarly restricted to perspectives from the ground, sightlines, especially on the high side of the road, were often open, and extensive efforts to find anoles at greater heights resulted in very few observations. Albeit based on largely anecdotal data, the suggestion that Grenadian anoles do not exploit perches at great heights to any substantive degree would indicate that the data generated during this study are representative. Also, because

treeboas are located by eliciting reflections from their eyes with headlamp beams, they could be located at heights extending to the top of the canopy.

We recorded the following data: species, sex, snout-vent length (SVL) to the nearest 0.5 mm, exact location, perch height in cm; perch diameter in mm; substrate type (leaf, branch, or both); orientation relative to the origin of the perch (toward, away, or neither, for example, for vines where the origin was not applicable); orientation relative to the ground (up, diagonal up, horizontal, diagonal down, or down); and, on the assumption that thorns might deter nocturnal predators, the presence or absence of thorns. Each lizard was uniquely marked with 1-3 variously colored bands of paint at the base of the tail and released at the location of capture. We were careful not to disturb other sleeping anoles or previously marked animals while collecting data.

We used the SCHNABEL (1938) method to estimate population sizes of both species along the transect and calculated population densities by extrapolating the densities for the two 6 x 40 m areas (0.024 ha) paralleling the road. We estimated structural niche breadths and niche overlaps based on perch heights and diameters using Levins' Meas-

ure (LEVINS 1968) and a Simplified Morisita's Index (HORN 1966), respectively. In addition, we calculated overlap based on a matrix that included both perch heights and diameters.

We tagged sleep-sites with surveyor's tape on which we noted the number of the individual lizard and calculated distances between sleep sites by triangulation after measuring heights above the ground and distance from the edge of the road.

We considered *A. aeneus* with SVL < 40 mm and *A. richardii* with SVL < 50 mm to be juveniles or subadults. This decision was based on data recorded for 25 lizards of both species collected at another comparable low-elevation site specifically to determine the minimum sizes at sexual maturity. All specimens collected were deposited in the Bobby Witcher Memorial Collection (BWMC), Avila University, Kansas City, Missouri 64145, USA. We conducted statistical analyses using StatView® 5.0 (SAS® Inst., Cary, North Carolina) and SYSTAT® 10.0 (SPSS® Inc., Chicago, Illinois). We used non-parametric tests unless data met all assumptions for the use of parametric tests. All means are presented \pm 1 standard error (SE); for all statistical tests, $\alpha = 0.05$.

RESULTS AND DISCUSSION

Size and sexual size dimorphism. Snout-vent lengths of *A. richardii* at the study site ranged from 46–95 mm for males and 43–69 mm for females, whereas SVL for *A. aeneus* ranged from 43–66 mm for males and 43–60 mm for females (table 1). We found very few juveniles (SVL < 30 mm), suggesting that reproduction is seasonal in these populations, with survivors from the previous year attaining adult size and hatchlings from the current year just beginning to appear. Sexual size dimorphism (SSD) indices based on maximum SVL were 1.38 for *A. richardii* and 1.29 for *A. aeneus*; adult:juvenile ratios were 2.9:1 for *A. richardii* and 7.2:1 for *A. aeneus*. STAMPS & CREWS (1976) determined that the peak of the *A. aeneus* egg-laying season is linked to the occurrence of rain. Since we conducted our study at the very beginning

of the rainy season, presumably few eggs had hatched, explaining the paucity of hatchlings. The difference in the relative frequency of juveniles between the two species might reflect an earlier onset of reproductive activity in *A. richardii* relative to *A. aeneus*.

Population sizes and densities. Population size and density estimates were 113 *A. richardii* (2354/ha) and 54 *A. aeneus* (1125/ha), with estimates of 72 *A. richardii* (3000/ha) and 33 *A. aeneus* (1375/ha) on the high side of the study site and 41 *A. richardii* (1708/ha) and 10 *A. aeneus* (417/ha) on the low side of the site. The high and low side totals do not add up for *A. aeneus* because SCHNABEL estimates are based on recaptures (or resightings) that can result in underestimates when dealing with smaller sample sizes. Significantly

Table 1: Sizes (SVL - Snout-Vent Length) and sleep-site perches of *Anolis richardii* DUMÉRIL & BIBRON, 1837 and *A. aeneus* GRAY, 1840 on Grenada. All data are presented \pm one standard error, range, and sample size (in parentheses).

Tab. 1: Körpergrößen (KRL - Kopf-Rumpf-Länge) und Schlafplätze von *Anolis richardii* DUMÉRIL & BIBRON, 1837 und *A. aeneus* GRAY, 1840 aus Grenada. Angegeben sind die Mittelwerte \pm 1 Standardabweichung, die Bereich Spannweite und die Anzahl (in Klammern).

| | All Alle | Males Männchen | Females Weibchen | Juveniles+Subadults Jungtiere+Subadulte |
|------------------------------------|----------------|-------------------|---------------------|--|
| <i>Anolis richardii</i> | | | | |
| SVL (mm) | 57.4 \pm 1.2 | 63.9 \pm 1.9 | 60.7 \pm 0.8 | 41.6 \pm 1.3 |
| KRL (mm) | 28-95 (106) | 50-95 (44) | 50-69 (35) | 28-49 (27) |
| Perch height (m) | 1.0 \pm 0.1 | 1.0 \pm 0.1 | 0.9 \pm 0.1 | 0.9 \pm 0.1 |
| Schlafplatz-Höhe (m) | 0.2-3.1 (103) | 0.2-3.1 (42) | 0.2-2.8 (35) | 0.3-2.4 (26) |
| Perch diameter (cm) | 3.0 \pm 0.3 | 3.7 \pm 0.5 | 2.9 \pm 0.3 | 2.2 \pm 0.4 |
| Astdurchmesser am Schlafplatz (cm) | 1-9 (46) | 1-9 (19) | 1-4 (15) | 1-6 (12) |
| <i>Anolis aeneus</i> | | | | |
| SVL (mm) | 49 \pm 1.3 | 54.4 \pm 1.5 | 46.3 \pm 0.6 | 32.2 \pm 5.3 |
| KRL (mm) | 21-66 (41) | 43-66 (20) | 43-51 (16) | 21-38 (5) |
| Perch height (m) | 1.2 \pm 0.2 | 1.7 \pm 0.2 | 1.8 \pm 0.2 | 1.6 \pm 0.5 |
| Schlafplatz-Höhe (m) | 1.0-3.2 (41) | 0.4-3.2 (20) | 0.4-3.0 (16) | 0.1-3.0 (5) |
| Perch diameter (cm) | 3.1 \pm 0.5 | 3.9 \pm 0.7 | 1.8 \pm 0.3 | 2.0 \pm 0 |
| Astdurchmesser am Schlafplatz (cm) | 1-8 (17) | 2-8 (10) | 1-3 (5) | - (2) |

more lizards of both species were found on the high side when compared with the low side (Mann-Whitney U; *A. aeneus*: $Z = -2.34$, $P = 0.02$, and *A. richardii*: $Z = -1.96$, $P < 0.05$). *Anolis richardii* was significantly more abundant than *A. aeneus* on both the high and low sides of the study site ($Z = -2.68$, $P = 0.006$; $Z = -2.94$, $P = 0.003$, respectively). The greater number on the high side probably is attributable to a greater number of available sleeping perches (see below), whereas the proportionately greater number of *A. richardii* on the low side is possibly attributable to the more densely shaded habitat in which these lizards appear to be more successful than *A. aeneus* (SCHOENER & GORMAN 1968; HARRIS et al. 2004).

When we compare our data with those of HARRIS et al. (2004), who conducted a concurrent, diurnal study of anoline densities and structural habitat use in completely comparable areas near our site, several substantive differences are evident. That our density estimates are considerably lower probably is attributable largely to the relative difficulty of finding all anoles in an area at night versus during the day. This is particularly applicable when dealing with lizards high above the ground, as individu-

als sleeping on leaves often are screened when viewed from beneath. When we compared the ratios of *A. richardii* with those of *A. aeneus* on the high and low sides, the ratios for *A. aeneus* were comparable (our data, 33:10 = 3.30 versus 3.47 for HARRIS et al. 2004; Contingency test, $df = 1$, $\chi^2 = 0.9$, $P = 0.35$), but those for *A. richardii* differed significantly (72:41 = 1.76 versus 0.41; $df = 1$, $\chi^2 = 103.6$, $P < 0.0001$). Individual *A. richardii* were either moving to the high side to take advantage of the apparently more abundant suitable sleeping sites there or, more likely, they were dispersing out of view into the higher branches of the larger trees on the low side. When we compared the ratios of *A. richardii* to *A. aeneus* on the low side, our data (41:10 = 4.10) were generally similar to those of HARRIS et al. (2004; 4.59), although they differed significantly ($df = 1$, $\chi^2 = 5.9$, $P = 0.02$). In contrast, the ratios on the high side (72:33 = 2.18 versus 0.54) differed dramatically ($df = 1$, $\chi^2 = 123.4$, $P < 0.001$), suggesting that individual *A. richardii* were moving to the high side at night.

Sleep-site characteristics. Both *A. aeneus* and *A. richardii* slept in a variety of positions and on various perch types (see tables 1 & 2). Individuals of both species

Table 2: Habitat utilization by sleeping *Anolis aeneus* GRAY, 1840 and *A. richardii* DUMÉRIE & BIBRON, 1837. Point of origin - Orientation relative to the leaf's/branch's point of origin.

Tab. 2: Habitatnutzung von schlafenden *Anolis aeneus* GRAY, 1840 und *A. richardii* DUMÉRIE & BIBRON, 1837. Sitzrichtung – Ausrichtung in bezug zum Ursprung des Blattes/Astes.

| Species (size class) | Orientation (↑:↗:→:↘:↓) Ausrichtung (↑:↗:→:↘:↓) | Thorns (present:absent) Stacheln (vorhanden:fehlend) | Perch (leaf:branch) Schlafplatz (Blatt:Zweig) | Point of origin (toward:away) Sitzrichtung (zum:weg vom) |
|---------------------------------------|--|---|--|---|
| <i>A. aeneus</i> | 17:17:12:13:15 | 6:66 | 29:35 | 11:59 |
| <i>A. richardii</i> (all/alle) | 18:24:88:68:78 | 10:244 | 123:132 | 148:66 |
| <i>A. richardii</i> (SVL/KRL > 80 mm) | 0:1:9:3:20 | 1:30 | 2:29* | ** |
| <i>A. richardii</i> (SVL/KRL < 80 mm) | 18:23:79:65:58 | 9:214 | 121:103 | 148:66 |

* most were woody stems of seedling trees / meistens holzige Stämmen von ganz jungen Bäumen.

** not applicable, all were on trunks or stems of trees / nicht anwendbar, da alle auf Baumstämmen waren.

usually were lying tight against the substrate (regardless of type) with eyes closed and hind limbs extended posteriorly. Individuals of both species and both large (SVL > 80 mm) and small (SVL < 80 mm) *A. richardii* slept on thornless perches significantly more frequently than on perches with thorns (Contingency tests; for all comparisons, $df=1$; $P < 0.001$). However, the differences were largely proportional to the abundance of thorny perches. The frequency of exploited thorn-laden perches did not differ significantly between large and small *A. richardii* ($\chi^2 = 0.2$, $P = 0.65$). *Anolis aeneus* were found on perches with thorns more frequently than *A. richardii* ($\chi^2 = 5.0$, $P = 0.03$).

The frequencies at which the smaller species, *A. aeneus*, used leaves or branches as sleep-sites did not differ significantly (Contingency test, $df = 1$, $\chi^2 = 1.0$, $P = 0.31$). Of those found on branches, a significant positive correlation existed between branch diameter and SVL (Kendall Rank Correlation, $Z = 2.54$, $P = 0.01$, $n = 35$), and perch diameters used by adult males were significantly greater than those used by adult females (Mann-Whitney U, $Z = 2.21$, $P = 0.03$, $n = 15$). Perch heights were not significantly correlated with SVL ($Z = 0.88$, $P = 0.38$, $n = 76$), nor did perch heights of males and females differ significantly ($Z = 0.61$, $P = 0.55$, $n = 36$).

Anolis aeneus most frequently faced away from the point of perch origin (84.3% of 70 observations). Frequencies of body orientation were horizontal (16.2% of 74 observations), diagonal up (23.0%), up

(23.0%), diagonal down (17.6%), and down (20.3%). Most were perched on plants that did not contain thorns (91.7% of 72 observations), in approximately the same proportion as the availability of thorny perches.

The frequencies at which the larger species, *A. richardii*, used leaves or branches as sleep-sites did not differ significantly (Contingency test, $df = 1$, $\chi^2 = 0.6$, $P = 0.43$), although the frequencies at which very large males (SVL > 80 mm) used leaves and branches did ($df = 1$, $\chi^2 = 25.1$, $P < 0.001$), undoubtedly because leaves were unable to support these large individuals. The only two large males found on leaves were on interwoven mats instead of single leaves. They most frequently were found facing away from the point of origin of the perch (69.2% of 214 observations). Frequencies of body position relative to the ground were variable, but horizontal and downward positions were most common. A significant positive relationship existed between SVL and perch diameter (Kendall Rank Correlation, $Z = 5.73$, $P < 0.0001$, $n = 144$), but no relationship existed between SVL and perch height ($Z = -1.10$, $P = 0.27$, $n = 278$). The mean perch height was 1.0 ± 0.1 m, with 61.3% perched < 1.0 m. No continuous variables differed statistically when grouped by sex. A t-test comparing perch heights of individuals with SVL > 80 mm and those with SVL < 80 mm showed that the largest lizards (exclusively males) perched significantly lower than smaller individuals (t-test, $t = 31.85$, $P = 0.00001$). This suggests an ontogenetic shift in perch height by male *A. richardii*.

Table 3: Nearest neighbor distances (a - *A. aeneus*, r - *A. richardii*, m - male, f - female, j - juvenile). Data are presented as means \pm one standard error, range (in parentheses), and sample size.

Tab. 3: Abstände (m) zum nächsten Nachbarn (a - *A. aeneus*, r - *A. richardii*, m - Männchen, f - Weibchen, j Jungtier). Angegeben sind die Mittelwerte \pm 1 Standardabweichung, Spannweite (in Klammern) und Anzahl.

| Relationship Beziehung | Distance to the nearest neighbor Abstand zum nächsten Nachbarn |
|---------------------------|---|
| af - af | 1.5 \pm 0.5 (0.7-2.4) 4 |
| am - af | 2.6 \pm 0.4 (1.8-3.2) 4 |
| am - aj | 1.9 \pm 0.5 (1.0-2.6) 3 |
| am - am | 2.2 \pm 0.9 (0.7-4.5) 4 |
| rf - af | 2.3 \pm 0.4 (0.8-9.0) 22 |
| rf - am | 2.4 \pm 0.3 (0-5.6) 23 |
| rf - rf | 2.3 \pm 0.2 (0.5-5.8) 47 |
| rf - rj | 2.8 \pm 0.5 (0.4-8.2) 16 |
| rj - am | . 0 \pm 0.1 (0.9-1.3) 5 |
| rj - rj | 2.1 \pm 0.5 (0.9-3.2) 5 |
| rm - af | 2.2 \pm 0.3 (0.9-5.2) 20 |
| rm - aj | 1.1 \pm 0.5 (0.6-2.1) 3 |
| rm - am | 2.2 \pm 0.3 (0.4-5.0) 2.7 |
| rm - rf | 2.3 \pm 0.2 (0-13.3) 76 |
| rm - rm | 2.2 \pm 0.2 (0.2-6.6) 40 |

Sleeping *A. richardii* perched significantly lower than *A. aeneus* (Mann-Whitney U, $Z = -3.30$, $P = 0.001$, $n = 95$). These data suggest that anoles behave very differently at night when compared to diurnal perch selection. SCHOENER & GORMAN (1968) noted that male *A. richardii* perch significantly higher than smaller conspecifics and *A. aeneus* of all sizes. ROUGHGARDEN et al. (1983) found no differences in perch heights at four different sites, and HARRIS et al. (2004) found that perch heights varied considerably in different habitats. However, no diurnal observations suggest that larger individuals (i.e., adult male *A. richardii*) perch lower than smaller congeners. Sleeping lower might suggest that larger animals seek out thicker, more stable perches, but we found several of the largest males sleeping on vines of very small diameter and diameters of perches used by large males and smaller lizards did not differ significantly ($Z = -0.92$, $P = 0.33$, $n = 49$). Neither SCHOENER & GORMAN (1968) nor HARRIS et al. (2004) reported significant differences in diurnal perch diameters among age classes or between species.

Based on perch diameter, Levin's measure of niche breadth of *A. aeneus* was

0.29, whereas that of *A. richardii* was 0.54. Based on perch height, niche breadth of *A. aeneus* was 0.66, whereas that of *A. richardii* was 0.41. When based on a matrix of perch diameters and heights, niche breadth of *A. aeneus* was 0.15 and that for *A. richardii* was 0.22. Simplified Morisita's measures of niche overlap between the two species, based on perch height, diameter, and a matrix of both variables, respectively, were 0.75, 0.73, and 0.60. Relatively high niche breadths and overlaps suggest that neither species is particularly selective when choosing nocturnal perches and that both species apparently use largely similar criteria when making such choices.

Spatial distribution. *Anolis richardii* and *A. aeneus* individuals were randomly distributed on both sides along the transect (Poisson Distribution, $df = 19$, *A. richardii*: high side, $\chi^2 = 29.37$; low side, $\chi^2 = 23.54$; *A. aeneus*: high side, $\chi^2 = 16.09$; low side, $\chi^2 = 23.55$, $P > 0.05$ for all tests).

We defined an individual's nearest neighbor as the closest anole, regardless of species (table 3). No distances between any sex or age categories of either species differed significantly (ANOVA, $df = 8$, $F = 0.33$, $P = 0.96$). Distances for all age and sex classes combined did not differ by species (Mann-Whitney U, $Z = -0.2$, $P = 0.84$), nor did intraspecific male-male and male-female distances for either species (*A. richardii* male-male versus male-female distances, $Z = -0.39$, $P = 0.70$; *A. aeneus* male-male versus male-female distances, $Z = -0.58$, $P = 0.56$). These data would indicate that the presence or absence of other anoles of either species has little or no effect on sleep-site selection.

Sleep-site fidelity. We encountered a total of 144 lizards throughout the study. Of these, we saw 54 *A. richardii* and 15 *A. aeneus* on consecutive nights (47.9% of the total), and 35 *A. richardii* and six *A. aeneus* on two or more consecutive nights (44.9% of lizards subsequently seen and 28.5% of all lizards marked). Of 13 male *A. richardii* observed on consecutive nights, six were within 1.0 m of the prior night's perch. Twelve of 17 *A. richardii* females and three of five juveniles had moved less than 1.0 m from the prior

night's site. Three male *A. aeneus*, two females, and one juvenile all had moved less than 1.0 m from the previous night's perch.

The mean maximum distance moved by individuals observed at least twice (but not necessarily on consecutive nights) was 2.6 ± 0.2 m for *A. richardii* ($n = 58$) and 4.7 ± 6.1 m for *A. aeneus* ($n = 16$). The latter figure includes one very large outlier; by omitting data for only one individual, the mean distance is 3.2 ± 2.7 m, which probably is more representative. However, even with the outlier included, maximum distances moved by the two species do not differ significantly (t-test, $t = 0.62$, $P = 0.55$). Male *A. aeneus* moved significantly farther than females (Mann-Whitney U, $Z = -2.15$, $P = 0.03$, $n = 9, 5$). Male *A. richardii* also moved farther than females, although differences were not significant ($Z = -1.87$, $P = 0.06$, $n = 22, 26$). This is suggestive of larger home ranges, but we do not know if larger individuals or even the largest males have larger home ranges, especially as they relate to sleep-site selection.

Our data do not support an assumption of high sleep-site fidelity. Fewer than 50% of the marked anoles were subsequently observed in the study site, and fewer than 30% were observed on consecutive nights. Although we encountered a few lizards ($n = 27$; 18.8% of the total number marked) within 1.0 m of the previous night's perch, this is insufficient to suggest that anoles strive to return to a specific sleep-site. These data differ dramatically from those of CLARK & GILLINGHAM (1990). For two species of *Anolis* on Puerto Rico, they observed that more than 96% of their study lizards were recaptured within 1.0 m of the original night's sleep site, and, at one site, 98% of

the lizards were recaptured within 1.0 m of the original sleep site for five consecutive nights.

Predatory habitat utilization. Thirty-seven of 55 marked *Corallus grenadensis* observed at or below 4.0 m perch height during a 120-person hour study at this site exhibited a mean perch height of 2.75 ± 0.20 m (R. W. HENDERSON, unpubl. data). Boas were not distributed uniformly throughout the habitat, but rather exhibited preferences for certain types of situations depending on size class (HENDERSON 2002). Anoles, however, were more or less infradispersed in three dimensions throughout the area. That anoles commonly assumed sleeping perches at heights at which boas forage was not surprising, although surveying for sleeping anoles perched above 4.0 m was visually and physically precluded by researchers working from the ground.

CLARK & GILLINGHAM (1990) listed a number of potential anole predators at their study site. Certainly some of the same nocturnal predators, or similar predators, occurred at our study site (e.g., whip scorpions, boas, roof rats). Both species of *Anolis* were virtually ubiquitous throughout our study site (and, indeed, most of Grenada; GERMANO et al. 2003) and, aside from sleeping on the distal ends of branches, we observed no obvious anti-predator strategies in either species. On the contrary, prolonged observations of sleeping anoles in close proximity to foraging treeboas suggest that they are seemingly unconcerned about the moving snakes (YORKS et al. 2004). Because of the ubiquity and density of both *Anolis* species, the likelihood of predation on any one individual is low, and therefore no species-specific anti-predator strategies, including fidelity to sleep sites, appear to have evolved.

CONCLUSIONS

Although *Anolis richardii* tended to utilize lower sleeping perches than *A. aeneus*, the variety of perches used by both species and the relatively high structural niche overlaps suggest that these two species do not partition available sleep sites, at least in these

habitats. However, this should not be construed to preclude the possibility of partitioning on the basis of factors we did not consider. Other than frequently sleeping on leaves or the distal ends of branches, we found no evidence that indicated that lizards selected

sleep sites or exhibited sleeping behaviors that minimized opportunities for predation by *Corallus grenadensis*, nor did we observe high levels of sleep-site fidelity for perches presumably less vulnerable to predation. Thus, our data supported none of our predictions, suggesting that the abundance of

essential resources at this site precludes a necessity for partitioning and that the resultant abundance of anoles sufficiently reduces the likelihood of predation on any individual that selective pressures favoring the evolution of anti-predator behaviors are weak or non-existent.

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