

## Anoles of St. Vincent (Squamata: Polychrotidae): Population Densities and Structural Habitat Use

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**ABSTRACT.**—We examined population densities and structural microhabitat use by *Anolis griseus* and *A. trinitatis* at eight sites on the leeward (western) coast of St. Vincent, West Indies. Estimates of population density based on the Schnabel method varied according to habitat complexity and ranged to 5,208/ha for *A. griseus* (a higher estimate at one site was not considered due to conditions that compromised the accuracy of estimates) and to 27,923/ha for *A. trinitatis*. Our highest estimate for both species at one site (32,867/ha) was the highest yet recorded for any site on a two-species Lesser Antillean island. For both species, larger individuals tended to perch higher and on perches of larger diameter than smaller lizards, with adult male *A. griseus* using the highest and largest diameter perches. However, considerable overlap in perch use among other size classes of *A. griseus* and all size classes of *A. trinitatis* suggests that structural habitat partitioning is not rigid in these two species. Although *A. griseus* was most abundant at densely shaded sites, *A. trinitatis* was essentially ubiquitous, supporting the predictions that these anoles were ecologically versatile and abundance and microhabitat use would reflect available vegetative structure.

**KEYWORDS.**—*Anolis griseus*, *Anolis trinitatis*, St. Vincent, population densities, structural habitat use.

### INTRODUCTION

Studies of behavioral and evolutionary ecology show that habitats occupied by individuals play a vital role in determining the fitness and evolutionary dynamics of the populations to which the organisms belong (Rosenzweig 1991; Rodríguez-Robles et al. 2005). Lesser Antillean *Anolis* lizards often adapt remarkably well to altered environments and are decidedly euryoecious (Henderson and Powell 1999, 2001; Powell and Henderson 2005). Ecological studies on West Indian anoles have shown that interspecific niche partitioning is clearly defined among ecomorphs (e.g., Rand and Williams 1969; Schoener and Gorman 1968; Schoener and Schoener 1971), and Losos et al. (1994) illustrated a tendency in anoles to continue adapting to the niches for which they are specialized.

St. Vincent (13°15' N, 61°12' W) is a rela-

tively small (ca. 344 km<sup>2</sup>) Lesser Antillean island of volcanic origin. Habitats range from dry scrub forest to rainforest at higher elevations. The highest elevation (La Soufrière Volcano) rises 1,234 m above sea level (asl). Average temperature ranges from 18–32°C and average annual rainfall ranges from 1,500 mm on the leeward side to 3,800 mm on the windward side. The topography of the island consists largely of steep slopes dissected by lush valleys, with relatively narrow coastal plains. Because of the harsh topography, many of the uplands were spared the extensive deforestation during the colonial era that occurred on Lesser Antillean islands with less relief (Callaghan 2007).

*Anolis griseus* and *A. trinitatis* are endemic to St. Vincent and, until recently, were the only anoles on the island. *Anolis sagrei* has only recently become established on St. Vincent (Henderson and Powell

2005; Treglia 2006), where it remains largely restricted to highly disturbed habitats at ports and in urban areas (Treglia et al., 2008). Both native anoles are widely distributed (Treglia 2006; Mallery et al. 2007; Powell and Henderson 2007). *Anolis griseus* is a large (maximum known SVL = 136 mm and 86 mm for males and females, respectively) arboreal lizard characterized by mossy gray-brown dorsal ground color with yellow-green tinges and dark V-shaped patterning across the dorsum. *Anolis trinitatis* is of medium size (SVL to 74 mm and 57 mm males and females, respectively), arboreal, and characterized by a bright green-yellow to blue-green coloration with mottled or herringbone mid-dorsal patterning (Schwartz and Henderson 1991). Previous ecological work on these species is limited to estimates of population densities (Roughgarden et al. 1983), brief synopses (Schwartz and Henderson 1991; Malhotra and Thorpe 1999; Treglia 2006), comments on conservation status (Powell and Henderson 2007), and notes on distribution (e.g., Heselhaus and Schmidt 1990; Corke 1992; Fläschendräger and Wijffels 1996; Mallery et al. 2007).

In June 2006, we examined relative abundances and microhabitat use in *A. griseus* and *A. trinitatis* at sites that differed considerably in vegetation, extent of insolation, and degree of human-mediated disturbance to test the predictions that ecologically versatile anoles adjust readily to local conditions and their habitat use will reflect available vegetative structure.

## METHODS

From 3-21 June 2006, at the onset of the rainy season, we studied anoline populations at eight different locations on the leeward (western) side of St. Vincent (Fig. 1, Table 1). Each site, chosen as characteristic of habitat in the area, consisted of two replicate 12 × 12 m (144 m<sup>2</sup>) quadrats of essentially homogenous habitat in order to increase sample sizes. All data were collapsed across the two replicates at each site so that each was treated as a single entity for purposes of statistical analysis. Two

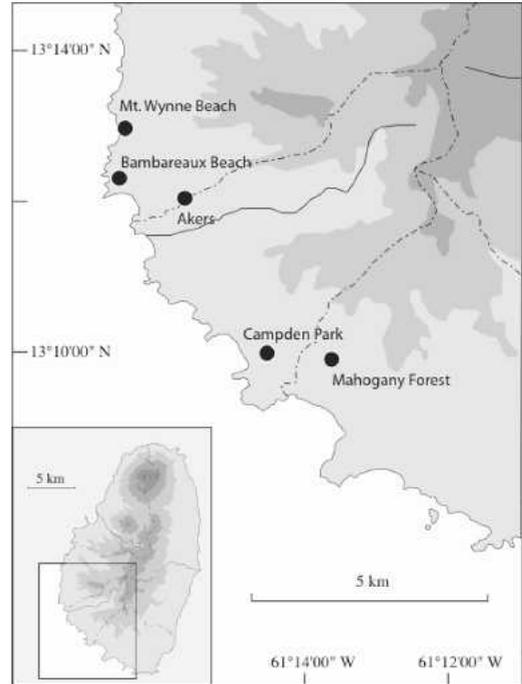


FIG. 1. Map of St. Vincent showing locations of study sites (Table 1). Two sites were located at the Campden Park locality and three at Mt. Wynne Beach.

individuals surveyed quadrats for thirty minutes twice per day for three consecutive days, once in the morning (0900-1100 h) and again in the afternoon (1400-1700 h). To estimate population sizes, we employed methods of Heckel and Roughgarden (1979), using spray guns to mark individual lizards each day with different colors of non-toxic latex paint diluted (1:1) with water. For each anole painted during a census, we recorded species (*A. trinitatis*, *A. griseus*), size class (adult male, subadult male/adult female, juvenile), perch diameter (cm), perch height (cm), perch type (tree, shrub, herbaceous, ground, rock, deadfall), orientation (up, down, horizontal), and degree of insolation (shade, partial shade, or full sun) at the location where the anole was first sighted. Size classes were defined according to sizes of individuals captured during a concurrent investigation at a site not sampled in this study: 1 = adult males (snout-vent length [SVL] > 75 mm for *A. griseus*, > 55 mm for *A. trinitatis*), 2 = subadult males and adult females, 3 = ju-

TABLE 1. Characterization of study sites on St. Vincent: **Site 1–Campden Park A** (~ 40 m): Disturbed, dry lowland, scrub-forest; **Site 2–Campden Park B** (~ 25 m): Disturbed, lowland plantation forest; **Site 3–Bambareaux** (<10 m): Moderately moist plantation forest consisting mostly of large Mango (*Mangifera* spp.) trees mixed with lowland dry forest; **Site 4–Akers** (200–260 m): Dry forest remnants bordered by recently cleared pastures; **Site 5–Mount Wynn A** (<10 m): Mixed palm plantation and pastureland consisting of Thorny (*Acrocomia aculeata*) and Coconut Palms (*Cocos nucifera*) and frequented by grazing cattle; **Site 6–Mount Wynn B** (<10 m): Flamboyant (*Delonix regia*) stand consisting of many saplings covered with vines; **Site 7–Mount Wynn C** (<10 m): Guava (*Psidium guajava*) plantation forest; **Site 8–Mahogany** (135 m): Reclaimed forest dominated by *Pinus* sp. and Mahogany (*Swietenia macrophylla*) and characterized by a very dense canopy. All values are percentages except “# Tree > 15 cm,” which is a count. “Debris” consists of accumulated piles of palm fronds and miscellaneous branches. See methods for explanation of “Density.”

Site	Shade (%)	Leaf litter (%)	Herbaceous (%)	Boulders (%)	Debris (%)	# Trees >15 cm	Vegetation density
1	60	60	60	25	20	16	10
2	50	45	50	3	5	16	2
3	85	50	70	0	25	25	8
4	80	75	20	0	10	26	8
5	30	5	25	5	30	11	2
6	35	20	15	0	15	1	6
7	60	50	25	5	10	1	10
8	95	60	40	15	7	10	8

veniles (SVL < 50 mm for *A. griseus*, < 40 mm for *A. trinitatis*). Due to the difficulty of distinguishing subadult males and females at a distance, these lizards were grouped into the same size class. Resultant data were used to estimate population densities (Schnabel 1938; Heckel and Roughgarden 1979) and quantify niche parameters by species and class. Because observations of individuals occurred on different days and anoles move, we treated observations as independent events for statistical analyses of perch data. Using litter, rocks and deadfall laying on the ground, and elevated perches (deadfall, trunks, branches, and vines) at 50 cm intervals as categories, we calculated Levins’ (1968) structural niche breadths (*B*) for each species and size class using the following equation:

$$B = \frac{1}{\sum I_x^2},$$

in which *I* represents the frequency of observations in each category. This measure was standardized (*B<sub>A</sub>*) on a scale of 0-1 using the following equation (Hurlbert 1978):

$$B_A = \frac{B - 1}{n - 1},$$

in which *n* equals the number of categories.

We also calculated standardized niche overlaps (*O*) between species and size classes in each habitat and for all habitats, using the following equations (modified from Pianka 1973):

$$O = \frac{\sum I_g I_t}{\sqrt{\sum I_g^2 \sum I_t^2}} \quad \text{and} \quad O = \frac{\sum I_1 I_2 I_3}{\sqrt{\sum I_1^2 \sum I_2^2 \sum I_3^2}},$$

in which *I<sub>g</sub>* and *I<sub>t</sub>* represent categories used by *A. griseus* and *A. trinitatis*, respectively, and *I<sub>1</sub>*, *I<sub>2</sub>*, and *I<sub>3</sub>* represent categories used by each size class of the species examined. For calculations involving perch diameters, we used only diameters of elevated perches with categories defined by the following ranges of measurements: ≤1 cm, >1-5 cm, >5-10 cm, >10-15 cm, >15-20 cm, >20-25 cm, >25-30 cm, and >30 cm.

To evaluate the density and composition of vertical structure available at each plot, we selected five trees used extensively by anoles within each plot and measured 2 m in each cardinal direction, recording the trunk diameter at breast height (dbh) and distance from the original tree of any vegetation in contact with that line. Based on these counts, each site was assigned a rank of increasing density from 1 to 10 (1 = no vertical trunks or hanging vines, 10 = densely

vegetated with vertical structure composed of tree trunks or hanging vines). We also categorized sites according to dominant plants (to genus), number of trees >15 cm dbh, and percent of area shaded, covered by herbaceous (non-woody) vegetation, and substrate littered with piles of deadfall (Table 1).

The shade, density, and height of the contiguous canopy at Site 8, complicated further by inclement weather, rendered accurate species identification of anoles extremely difficult. We also experienced problems recognizing previously marked animals. Consequently, we deemed data generated there to be unreliable and excluded them from statistical analyses. However, due to unique qualities of the site, we chose to include separately some discussion of results generated there.

We used StatView® 5.0 (SAS Institute Inc., Cary, North Carolina) for all statistical tests. Means are reported ± SE, except population estimates based on the Heckel and Roughgarden (1979) method, which we present ± one SD. For all tests, α = 0.05.

RESULTS

We recorded 207 observations of *A. griseus* that were suitable for statistical analyses. These were limited to four sites (we marked only one male in plot 5 and treated animals marked in plot 8 separately). We recorded 1,864 suitable observations of *A. trinitatis*. These anoles were ubiquitous in all eight surveyed sites. We omitted from any statistical analyses data that we recorded for 22 individuals that we were unable to identify to species.

Estimates of population sizes and densities (Table 2) show that *A. griseus* was most abundant at sites 8, 6, and 3, and that *A. trinitatis* was most abundant at sites 3, 5, and 2.

Perch heights (Table 3) of *A. griseus* were significantly higher than those of *A. trinitatis* across age classes at all sites for each species combined (Mann Whitney U, Z = -3.63, P = 0.0003). Perch heights of *A. griseus* (Fig. 2) of different size classes varied significantly (ANOVA, F = 12.22, df = 2, all

TABLE 2. Population size and density estimates (per ha; in parentheses) for *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

Species	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
<i>A. griseus</i>	—	18.8 ± 0.23 (1,305)	71.2 ± 0.12 (4,944)	64.7 ± 0.12 (4,493)	Only 1 male (69)	75.5 ± 0.12 (5,208)	—	138.5 ± 0.08 (9,618)
	—	13.7 ± 2.7 (951)	92.6 ± 17.3 (6,430)	76.8 ± 15.4 (5,333)	Only 1 male (69)	53.4 ± 30.8 (3,708)	—	—
<i>A. trinitatis</i>	110.6 ± 0.10 (7,680)	329.6 ± 0.06 (22,888)	402.1 ± 0.05 (27,923)	185.8 ± 0.07 (12,902)	374.8 ± 0.05 (26,027)	270.5 ± 0.06 (18,784)	226.6 ± .07 (15,736)	37.6 ± 0.16 (2,611)
	101.7 ± 2.4 (7,013)	548.8 ± 120.7 (38,111)	410.7 ± 40.2 (28,520)	185.9 ± 14.2 (12,909)	—	355.6 ± 42.0 (24,694)	—	44.9 ± 17.3 (3,118)

Estimates based on the Schnabel (1938) equation (± 1 SE) are presented first and estimates based on the Heckel and Roughgarden (1979) method (± 1 SD) are listed beneath. Dashes indicate the absence of the species at that site or insufficient data to make an estimate.

TABLE 3. Perch heights of *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

<i>Anolis griseus</i>									
Size class	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	All*
1	—	343.8 ± 90.6 40-650 N = 8 (0)	148.7 ± 15.8 0-300 N = 23 (1)	220.0 ± 38.4 30-400 N = 10 (0)	—	245 ± 33 120-400 N = 10 (0)	—	349.0 ± 38.2 0-800 N = 29 (1)	212.2 ± 20.4 0-650 N = 51 (1)
2	—	100.0 ± 57.7 0-200 N = 3 (1)	138.5 ± 22.4 0-350 N = 24 (3)	143.0 ± 18.8 0-350 N = 24 (1)	—	122.0 ± 32.5 40-200 N = 5 (1)	—	193.7 ± 30.8 0-500 N = 20 (1)	136.9 ± 13.0 0-350 N = 56 (6)
3	—	10.0 ± 6.3 0-30 N = 5 (3)	79.5 ± 23.9 0-250 N = 11 (3)	94.6 ± 25.4 0-250 N = 12 (3)	—	166.0 ± 64.9 0-400 N = 5 (1)	—	60.4 ± 23.3 0-200 N = 9 (1)	87.6 ± 16.7 0-400 N = 33 (10)
All	—	193.8 ± 59.7 0-650 N = 16 (4)	131.3 ± 12.4 0-350 N = 58 (7)	147.1 ± 15.5 0-400 N = 46 (4)	—	194.5 ± 26.1 0-400 N = 20 (2)	—	250.7 ± 26.1 0-800 N = 58 (3)	152.7 ± 10.7 0-650 N = 140 (17)
<i>Anolis trinitatis</i>									
1	96.1 ± 12.2 0-400 N = 51 (4)	127.8 ± 17.1 0-500 N = 73 (18)	165.9 ± 13.2 0-660 N = 72 (4)	205.2 ± 18.2 30-600 N = 45 (0)	196.2 ± 12.1 30-500 N = 93 (0)	146.2 ± 10.1 0-500 N = 112 (5)	150.6 ± 14.6 0-400 N = 47 (1)	87.5 ± 12.5 75-100 N = 2 (0)	156.1 ± 5.4 0-660 N = 494 (32)
2	57.7 ± 6.5 0-350 N = 96 (19)	64.8 ± 8.5 0-450 N = 155 (72)	126.3 ± 7.3 0-400 N = 140 (9)	121.1 ± 11.7 0-550 N = 93 (12)	124.2 ± 6.5 0-450 N = 217 (20)	119.7 ± 6.6 0-500 N = 213 (15)	106.5 ± 7.4 0-350 N = 120 (5)	275.0 ± 75.0 200-350 N = 2 (0)	105.9 ± 3.0 0-550 N = 1036 (152)
3	33.1 ± 12.2 0-220 N = 23 (7)	17.3 ± 3.6 0-200 N = 87 (56)	105.8 ± 14.4 0-250 N = 28 (5)	83.9 ± 22.4 0-350 N = 18 (6)	115.3 ± 15.6 0-350 N = 24 (1)	112.2 ± 17.3 0-400 N = 34 (11)	94.7 ± 12.6 0-300 N = 43 (1)	69.2 ± 21.1 6-200 N = 9 (0)	126.3 ± 4.2 0-660 N = 748 (87)
All	65.9 ± 5.6 0-400 N = 170 (30)	66.3 ± 6.2 0-500 N = 315 (146)	135.8 ± 6.2 0-660 N = 241 (18)	141.1 ± 9.7 0-600 N = 156 (18)	143.6 ± 5.8 0-500 N = 334 (21)	127.2 ± 5.3 0-500 N = 359 (31)	113.9 ± 6.1 0-400 N = 210 (7)	103.7 ± 27.0 6-350 N = 13 (0)	114.5 ± 2.5 0-660 N = 1785 (271)

Mean perch heights (cm) are listed ± 1 SE, followed by ranges and sample sizes, with the number of individuals observed on the ground in parenthesis. Size classes: 1 = adult males, 2 = subadult males/adult females, 3 = juveniles. Dashes indicate missing values. \*Site 8 is excluded from this column (see text).

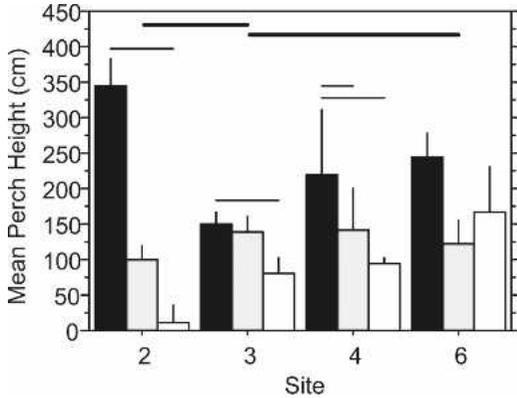


FIG. 2. Mean perch heights ( $\pm 1$  SE) of three size classes of *Anolis griseus* at four study sites on St. Vincent (Table 1) where we marked more than one individual (black bars = adult males, gray bars = subadult males/adult females, white bars = juveniles). Horizontal lines indicate significant differences (Fisher's PLSD,  $P < 0.05$ ) between sites (bold lines) and size classes at each site (narrow lines). For example, the first bold line indicates a significant difference between sites 2 and 3, and the first narrow line indicates a significant difference between adult males and juveniles at site 2.

$P < 0.0001$ ), with males perching higher than subadult males/females and subadult males/females generally higher than juveniles. However, perch heights of all age classes combined did not differ across sites where we marked more than one individual ( $F = 1.92$ ,  $df = 2$ ,  $P = 0.13$ ). Perch heights of *A. trinitatis* (Fig. 3) of different size classes varied significantly ( $F = 71.48$ ,  $df = 2$ ,  $P < 0.0001$ ), showing the same pattern among size classes as seen in *A. griseus*. Also, perch heights of *A. trinitatis* of all age classes combined varied significantly across all sites ( $F = 27.81$ ,  $df = 6$ , all  $P < 0.0001$ ), with the greatest mean perch heights observed at sites characterized by an abundance of vertical structure (e.g., trunks, vines) and lowest where trees were fewer in number and debris (e.g., natural piles of vegetation, discarded appliances, trash, and other human detritus) was plentiful.

Sixteen of 140 (11.4%) *A. griseus* at the four sites where we marked more than one animal were on the ground. Of these, one (6.3%) was an adult male and ten (62.5%) were juveniles. For *A. trinitatis*, 271 of 1784

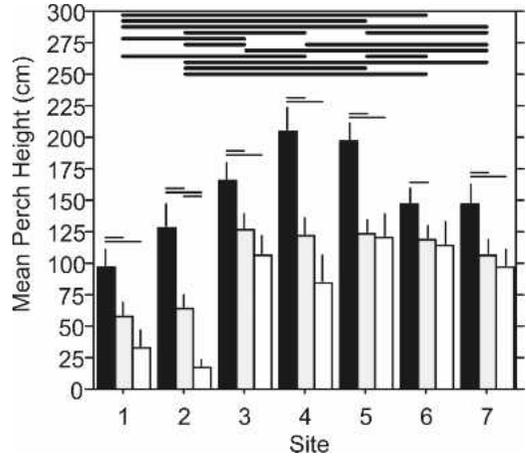


FIG. 3. Mean perch heights ( $\pm 1$  SE) of three size classes of *Anolis trinitatis* at seven study sites on St. Vincent (Table 1) (black bars = adult males, gray bars = subadult males/adult females, white bars = juveniles). Horizontal lines indicate significant differences (Fisher's PLSD,  $P < 0.05$ ) between sites (bold lines) and size classes at each site (narrow lines).

(15.2%) marked animals were on the ground. Of these 32 (11.8%) were adult males and 87 (32.1%) were juveniles. The proportion of lizards on the ground did not vary significantly by species (Contingency test,  $\chi^2 = 1.45$ ,  $df = 1$ ,  $P = 0.23$ ). The proportions of adult males, subadult males/adult females, and juveniles on the ground varied significantly for both *A. griseus* ( $\chi^2 = 16.70$ ,  $df = 2$ ,  $P = 0.0002$ ) and *A. trinitatis* ( $\chi^2 = 98.63$ ,  $df = 2$ ,  $P < 0.0001$ ), with adult males least likely and juveniles most likely to be found on the ground.

We found 7 of 58 *A. griseus* on the ground at site 3, 4 of 16 at site 2, 4 of 46 at site 4, and 1 of 20 at site 6; proportions did not differ significantly ( $\chi^2 = 3.05$ ,  $df = 3$ ,  $P = 0.38$ ), although sample sizes were very small. For *A. trinitatis*, percentages of individuals of all ages at seven sites ranged from 3.3% (site 7) to 46.3% (site 2), and proportions on the ground varied significantly ( $\chi^2 = 303.52$ ,  $df = 6$ ,  $P < 0.0001$ ).

When we examined elevated perch selection, all size classes of both *A. griseus* and *A. trinitatis* used woody plants significantly more frequently than herbaceous plants (Wilcoxon Signed-Rank test,  $Z = -2.20$ ,  $P = 0.03$ ), although the latter were more abundant than the former at all sites.

Diameters of perches (Table 4) used by *A. griseus* of different size classes varied significantly (ANOVA,  $F = 25.27$ ,  $df = 2$ , all  $P < 0.0001$ ). Perch diameters of *A. griseus* (Fig. 4) of all age classes varied significantly across sites (ANOVA,  $F = 10.54$ ,  $df = 3$ ,  $P < 0.0001$ ). Diameters of perches used by *A. trinitatis* of different size classes varied significantly ( $F = 71.48$ ,  $df = 2$ , all  $P < 0.0001$ ). Perch diameters of *A. trinitatis* (Fig. 5) of all age classes combined varied significantly across sites ( $F = 63.93$ ,  $df = 6$ ,  $P < 0.001$ ). Diameters of perches used by the two species when data for all age classes and all sites were combined did not differ significantly ( $F = 0.13$ ,  $df = 1$ ,  $P = 0.71$ ).

Calculated niche breadths (Table 5) based on perch heights for both species were wider than those based on perch diameters, and those of adult males were

generally wider than those for subadult males/females, with those of juveniles almost invariably the narrowest. For perch heights, niche breadths ranged from 0.07 (juvenile *A. griseus* at site 6) to 0.67 (all *A. trinitatis* at site 4). Niche breadths based on perch diameters ranged from 0.08 (juvenile *A. trinitatis* at site 7) to 0.61 (all *A. griseus* at site 4). Neither breadths based on heights (Mann Whitney U,  $Z = -0.47$ ,  $P = 0.64$ ) nor those based on diameters ( $Z = -0.85$ ,  $P = 0.39$ ) differed significantly by species.

Calculated niche overlaps between size classes (Table 6) were higher for *A. trinitatis* than for *A. griseus*, although differences were not significant (Mann Whitney U; height:  $Z = -1.55$ ,  $P = 0.12$ ; diameter:  $Z = -1.35$ ,  $P = 0.18$ ). The lower values for *A. griseus* may be attributable to low sample sizes of some size classes at several sites.

TABLE 4. Perch diameters used by *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

<i>Anolis griseus</i>									
Size class	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	All*
1	—	56.1 ± 10.5 3-90 N = 8	10.4 ± 2.0 1-40 N = 22	27.7 ± 5.8 4-65 N = 10	—	16.1 ± 8.6 1-90 N = 10	—	21.6 ± 2.0 3-40 N = 28	22.3 ± 3.5 1-90 N = 50
2	—	30.0 ± 6.0 24-36 N = 2	9.4 ± 2.0 1-30 N = 20	15.7 ± 4.0 1-80 N = 22	—	8.0 ± 4.3 1-24 N = 5	—	12.3 ± 2.0 2-25 N = 18	13.0 ± 1.8 1-80 N = 49
3	—	5.0 ± 4.0 1-9 N = 2	16.2 ± 6.1 1-40 N = 8	17.3 ± 7.3 1-65 N = 9	—	11.8 ± 4.4 1-20 N = 4	—	19.0 ± 6.5 3-45 N = 7	14.9 ± 3.6 1-65 N = 23
All	—	43.2 ± 9.1 1-90 N = 12	10.9 ± 1.5 1-40 N = 50	19.0 ± 3.1 1-80 N = 41	—	13.1 ± 4.7 1-90 N = 19	—	18.1 ± 1.6 2-45 N = 53	17.2 ± 1.8 1-90 N = 122
<i>Anolis trinitatis</i>									
1	18.4 ± 3.3 2-90 N = 44	51.5 ± 5.1 1-150 N = 53	9.0 ± 1.2 1-40 N = 66	17.3 ± 2.3 1-60 N = 45	29.5 ± 1.7 1-70 N = 93	13.0 ± 1.5 1-80 N = 107	4.4 ± 0.3 1-10 N = 46	13.5 ± 6.5 7-20 N = 2	20.3 ± 1.1 1-150 N = 455
2	11.0 ± 1.7 1-75 N = 76	39.7 ± 4.7 1-150 N = 83	7.2 ± 0.8 1-60 N = 122	15.3 ± 1.9 1-69 N = 89	22.6 ± 1.3 1-70 N = 194	10.0 ± 0.9 1-65 N = 197	10.9 ± 1.3 1-60 N = 115	12.0 ± 0.0 4-20 N = 2	15.9 ± 0.7 1-150 N = 870
3	7.5 ± 3.2 1-45 N = 14	11.5 ± 4.1 1-90 N = 29	6.7 ± 2.3 1-40 N = 23	11.5 ± 3.5 1-36 N = 12	16.7 ± 3.8 1-48 N = 23	7.4 ± 1.7 1-50 N = 32	4.0 ± 0.5 1-20 N = 42	4.4 ± 2.0 1-20 N = 9	17.2 ± 0.9 1-150 N = 139
All	13.1 ± 1.5 1-90 N = 134	38.5 ± 3.1 1-150 N = 165	7.7 ± 0.7 0-60 N = 212	15.6 ± 1.4 1-70 N = 138	24.2 ± 1.0 1-70 N = 310	10.7 ± 0.7 1-80 N = 336	8.0 ± 0.8 1-60 N = 203	7.0 ± 2.1 1-20 N = 13	16.4 ± 0.6 1-150 N = 1498

Mean perch diameters (cm) are listed ± 1 SE, followed by ranges and sample sizes. Size classes: 1 = adult males, 2 = subadult males/adult females, 3 = juveniles). Dashes indicate missing values. \*Site 8 is excluded from this column (see text).

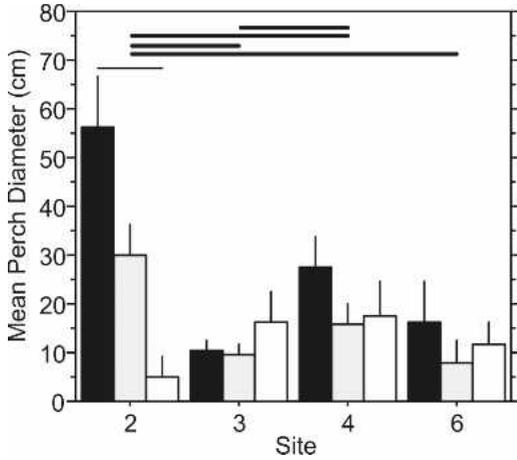


FIG. 4. Mean perch diameters ( $\pm 1$  SE) of three size classes of *Anolis griseus* at four study sites on St. Vincent (Table 1) where we marked more than one individual (black bars = adult males, gray bars = subadult males/adult females, white bars = juveniles). Horizontal lines indicate significant differences (Fisher's PLSD,  $P < 0.05$ ) between sites (bold lines) and size classes at each site (narrow lines).

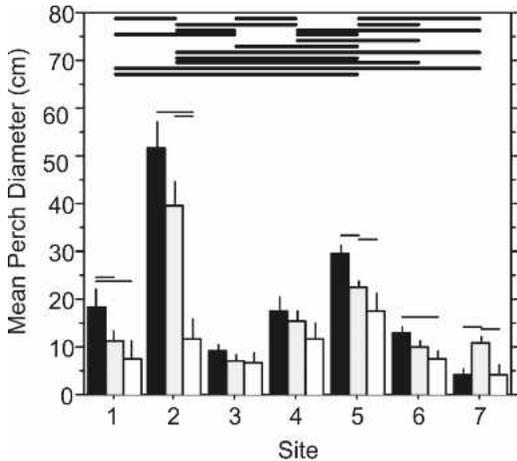


FIG. 5. Mean perch diameters ( $\pm 1$  SE) of three size classes of *Anolis trinitatis* at seven study sites on St. Vincent (Table 1) (black bars = adult males, gray bars = subadult males/adult females, white bars = juveniles). Horizontal lines indicate significant differences (Fisher's PLSD,  $P < 0.05$ ) between sites (bold lines) and size classes at each site (narrow lines).

Overlaps for *A. trinitatis* were very high (except for those based on height at site 2), with the lowest values for those based on both perch heights and diameters generally between adult males and juveniles.

TABLE 5. Structural niche breadths of *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

Species	Niche breadths based on perch heights							
	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	
<i>A. trinitatis</i>	<b>0.20</b> 0.43, 0.25, 0.14	<b>0.26</b> 0.55, 0.26, 0.12	<b>0.51</b> 0.66, 0.54, 0.46	<b>0.67</b> 0.66, 0.55, 0.40	<b>0.58</b> 0.59, 0.56, 0.31	<b>0.53</b> 0.59, 0.52, 0.44	<b>0.41</b> 0.52, 0.40, 0.30	
<i>A. griseus</i>	—	<b>0.44</b> 0.21, 0.22, 0.10	<b>0.60</b> 0.48, 0.49, 0.40	<b>0.58</b> 0.14, 0.57, 0.43	—	<b>0.58</b> 0.32, 0.20, 0.07	—	
<i>A. trinitatis</i>	<b>0.41</b> 0.52, 0.33, 0.19	<b>0.30</b> 0.19, 0.31, 0.13	<b>0.21</b> 0.28, 0.20, 0.10	<b>0.40</b> 0.49, 0.42, 0.36	<b>0.36</b> 0.31, 0.36, 0.22	<b>0.32</b> 0.43, 0.29, 0.21	<b>0.14</b> 0.09, 0.19, 0.08	
<i>A. griseus</i>	—	<b>0.18</b> 0.47, 0.17, 0.17	<b>0.45</b> 0.41, 0.46, 0.32	<b>0.61</b> 0.43, 0.58, 0.27	—	<b>0.32</b> 0.25, 0.21, 0.28	—	

Each entry contains four figures, which are standardized niche breadths (see text) for all individuals (bold) and for size classes 1-3 (1 = adult males, 2 = subadult males/adult females, 3 = juveniles). Dashes represent the absence of the species at that site. Data for site 8 are not included (see text).

TABLE 6. Structural niche overlaps of *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

Niche overlaps based on perch heights									
Species	Size class	Sites							
		1	2	3	4	5	6	7	All
<i>A. griseus</i>	1-2	—	0	0.73	0.59	—	0	—	0.74
	1-3	—	0.24	0.78	0.31	—	0	—	0.52
	2-3	—	0	0.76	0.63	—	0.63	—	0.81
<i>A. trinitatis</i>	1-2	0.85	0.39	0.91	0.75	0.87	0.94	0.95	0.93
	1-3	0.62	0.21	0.72	0.50	0.84	0.95	0.91	0.78
	2-3	0.74	0.17	0.82	0.61	0.93	0.96	0.98	0.93
Niche overlaps based on perch diameters									
<i>A. griseus</i>	1-2	—	0.72	0.95	0.47	—	0.95	—	0.90
	1-3	—	0.10	0.72	0.75	—	0.58	—	0.94
	2-3	—	0	0.77	0.76	—	0.49	—	0.73
<i>A. trinitatis</i>	1-2	0.86	0.92	0.99	0.93	0.89	0.99	0.97	0.97
	1-3	0.81	0.96	0.96	0.89	0.79	0.97	0.99	0.90
	2-3	0.97	0.73	0.97	0.97	0.97	0.98	0.97	0.97

Size classes: 1 = adult males, 2 = subadult males/adult females, 3 = juveniles. Dashes represent the absence of the species at that site. Data for site 8 are not included (see text).

Calculated niche overlaps based on perch heights between size classes of both species (Table 7) ranged from 44.2 (between adult male *A. griseus* and juvenile *A. trinitatis*) to 88.2 (adult female/subadult male *A. griseus* and adult male *A. trinitatis*). Overlaps based on perch diameters ranged from 55.6 (between adult male *A. griseus* and juvenile *A. trinitatis*) to 91.0 (juvenile *A. griseus* and adult male *A. trinitatis*).

Although fully insolated portions of sites ranged from 5-70% ( $\bar{x} = 38.1 \pm 8.3\%$ ), all *A. griseus* recorded in the survey were either in partial or full shade (55% and 45%, respectively; Table 8). No individuals were seen in direct sunlight. The majority of *A. trinitatis* were observed in partial shade (74%), several in full shade (23%), and very few in direct sunlight (3%).

Most adult male *A. griseus* were oriented

TABLE 7. Structural niche overlaps between *Anolis griseus* and *A. trinitatis* from eight study sites on St. Vincent (Table 1).

Niche overlaps based on perch heights					
Species	Size class	<i>A. trinitatis</i>			All
		1	2	3	
<i>A. griseus</i>	1	0.69	0.55	0.40	0.80
	2	0.88	0.81	0.68	
	3	0.66	0.84	0.88	
	All				
Niche overlaps based on perch diameters					
Species	Size class	<i>A. trinitatis</i>			All
		1	2	3	
<i>A. griseus</i>	1	0.80	0.73	0.56	0.77
	2	0.73	0.68	0.62	
	3	0.91	0.89	0.73	
	All				

TABLE 8. Orientation on and insolation of perches used by *Anolis griseus* and *A. trinitatis* at eight study sites on St. Vincent (Table 1).

Species	Size class	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	All*
Orientation (down–horizontal–up)										
<i>A. griseus</i>	1	—	2-1-5	12-2-9	3-0-5	—	5-1-4	—	25-1-3	47-5-26
	2	—	1-1-1	11-9-4	11-3-9	—	2-2-1	—	15-2-3	40-17-18
	3	—	0-4-1	7-3-1	7-5-0	—	3-1-1	—	2-2-5	19-15-8
	All	—	3-6-7	30-14-14	21-8-14	—	10-4-6	—	42-5-11	106-37-52
<i>A. trinitatis</i>	1	24-8-19	23-30-20	35-17-20	25-5-15	47-7-39	60-11-41	24-6-18	2-0-0	240-84-172
	2	39-27-30	41-88-25	68-35-37	57-19-17	103-51-64	127-27-59	75-13-32	2-0-0	512-260-264
	3	7-12-4	14-61-12	19-7-3	5-10-3	15-4-4	25-4-4	30-2-10	4-0-5	119-100-45
	All	70-47-53	78-179-57	122-59-60	87-34-35	165-62-107	212-42-104	129-21-60	8-0-5	871-444-481
Insolation (full sun–filtered shade–full shade)										
<i>A. griseus</i>	1	—	0-5-3	0-14-9	0-7-3	—	0-9-1	—	0-0-29	0-35-45
	2	—	0-3-0	0-18-6	0-21-2	—	0-5-0	—	0-0-20	0-47-28
	3	—	0-4-1	0-6-5	0-11-1	—	0-5-0	—	0-0-9	0-26-16
	All	—	0-12-4	0-38-20	0-40-6	—	0-19-1	—	0-0-58	0-108-89
<i>A. trinitatis</i>	1	4-17-30	4-46-23	0-51-21	1-44-0	0-74-19	4-95-13	0-43-5	0-0-2	13-370-113
	2	7-45-46	19-96-40	0-85-58	0-79-14	2-176-40	5-186-22	5-100-15	0-0-2	38-767-237
	3	1-11-11	6-50-23	0-14-14	0-17-1	1-16-6	1-30-2	0-41-1	0-0-9	9-179-67
	All	12-73-87	29-192-86	0-150-93	1-140-15	3-266-65	10-311-37	5-184-21	0-0-13	60-1316-417

Size classes: 1 = adult males, 2 = subadult males/adult females, 3 = juveniles). Dashes indicate missing values.

down (61%) or up (33%), with very few oriented horizontally (6%). Subadult males and females also were oriented down (53%) or up (24%) most frequently, although the numbers on horizontal perches (23%) were higher than for adult males. The largest number of juveniles (45%) were oriented down, and far fewer (19%) were oriented up than horizontally (36%).

Adult male *A. trinitatis* orientations were similar to that of adult male *A. griseus* with 48% oriented down, 35% up, and few (17%) oriented horizontally. Nearly half (49%) of the subadult males/females were oriented down, and percentages of those oriented up or horizontally were similar (both 25%). Like juvenile *A. griseus*, the largest number of juveniles (45%) were oriented down, and far fewer (17%) were oriented up than horizontally (38%).

#### DISCUSSION

*Population sizes and densities.*—*Anolis griseus* is an extremely wary lizard that escapes high into canopies at the slightest disturbance (Schwartz and Henderson 1991, Gorman 1968, Lazell 1972). The difficulty of spotting and marking these lizards from the ground undoubtedly compromised our results. Similar problems have confounded surveys of arboreal snakes (e.g., Powell et al., 2007), lizards (e.g., Reagan 1992; Harris et al. 2004), and amphibians (e.g., Guayasamin et al. 2006). Future studies might benefit greatly from canopy surveys, such as those implemented by Reagan (1992). Also, none of our sites were closed populations, resulting in estimates of population sizes that undoubtedly included animals on the margins of plots and overestimated total numbers. However, our methods were applied consistently and the resultant data are useful for comparisons of sites or with other studies using the same methods (e.g., Harris et al. 2004; Medina Díaz et al. 2005). Our density estimates for *A. griseus* (0-9,618/ha;  $\bar{x} = 3,205 \pm 1,223$ /ha) at most sites coincide closely with those from a previous study (5500/ha; Roughgarden et al. 1983). Counts at some sites and even the mean for all sites for *A. trinitatis* (2,611-38,111/ha;  $\bar{x} = 16,819 \pm 3,136$ /ha), however, are dramati-

cally higher than previous studies on the species (5000/ha; Roughgarden et al. 1983). The highest previous estimates for Lesser Antillean anoles that were based on similar methods are for *A. richardii* (12,750/ha on Grenada; Harris et al. 2004) and *A. gingivinus* (12,980/ha on St. Martin/St. Maarten; Roughgarden et al. 1983). Our highest estimates for both species at one site (site 3; 32,867/ha) exceeds the previous maximum recorded for anoles on two-species islands (Harris et al. 2004; 15,090/ha; *A. richardii* and *A. aeneus* at one site on Grenada). Notable is the fact that both the St. Vincent and Grenada sites were in relatively moist lowland forest with mixed agriculture (e.g., mango, citrus). Gorman and Harwood (1977) gave estimates of up to 20,000/ha for *A. pulchellus* on Puerto Rico, and Reagan (1992) gave a maximum of 25,870/ha for *A. stratulus*, also on Puerto Rico. The multi-species anoline communities at some sites on Puerto Rico (Reagan 1992) and possibly those on other Greater Antillean islands may exceed in total numbers of individuals in the two-species community at Bambarreaux (site 3) on St. Vincent.

These data suggest that *A. trinitatis* is exceedingly tolerant of variable conditions and habitats, whereas *A. griseus* prefers a more narrowly defined subset of habitat characteristics. The highest population counts for both species were in drastically different habitats. The very high numbers of *A. trinitatis* at site 5 reflects a high proportion of juveniles. Jenssen et al. (1998) postulated that juvenile *A. carolinensis* might be displaced to less optimal microhabitats by large males that dominate the best perches, and *A. trinitatis* may be doing the same thing. Adults, especially males, used the tall palms, whereas juveniles generally avoided tall trees, but were abundant in tall grass and piles of vegetative debris. High counts of *A. griseus* at site 8 presumably illustrate a preference by these lizards for high perches on large trees and full shade (Schwartz and Henderson 1991; Gorman 1968; Lazell 1972), which were abundant at that site. The other two sites with the highest counts for both species were similar in having several tall trees, but differed drastically in amount of shrubs, mois-

ture, and insolation. Site 6, with mid-range counts for both species, was a stand of tall, thin trees laden with vines that substantially increased available vertical structure. The canopy was very open, largely insolated, and relatively dry. All other sites where we found *A. griseus* had relatively contiguous canopies providing dense shade and were consequently moister. Such differences are largely qualitative, but are useful in noting differing degrees of tolerance by the two species for varying vegetative structures.

*Structural habitat use.*—Woody substrates were chosen over non-woody substrates by both species, supporting conclusions by Rodríguez-Robles et al. (2005), who indicated that anoles choose perch sites in a non-random fashion to best match their morphological adaptations. Beuttell and Losos (1999) suggested that *A. trinitatis* most closely resembles trunk-crown anoles and that *A. griseus* is most similar to crown-giants. Trunk-crown anoles tend to be ecologically versatile (Lenart et al. 1997; Losos and de Queiroz 1997; Powell 1999), and *A. trinitatis* appears to follow that pattern, effectively utilizing any available vegetative structures at varying sites, as demonstrated by the high structural niche breadths evident in this study. Crown-giants are generally less inclined to exploit the full extent of available microhabitats (Lenart et al. 1997). However, *A. griseus*, although apparently absent from some sites and despite an evident preference for large trees, showed considerable variation in habitat use where present in appreciable numbers. Whether this reflects ecological release (e.g., Losos and de Queiroz 1997) or the lack of selective constraints that would be imposed by the presence of multiple sympatric congeners is unknown.

Although perch heights and diameters varied considerably by site, some general trends were evident. Males of both species preferentially selected perches at greater heights and of larger diameters than did either subadult males/females or juveniles. These results coincide with a general trend that body sizes of anoles are positively correlated with higher and larger substrates (e.g., Schoener and Schoener 1971; Perry

1996; Janssen et al. 1998). Our results reflect previous suggestions that *A. griseus* prefers large trees and rarely descends to the ground, whereas *A. trinitatis* usually perches under 3 m (Schwartz and Henderson 1991; Malhotra and Thorpe 1999). These data are similar to those for Grenada (Harris et al. 2004) and St. Eustatius (Medina Díaz et al. 2005), which, like St. Vincent, have two native anoles. On both islands, the larger species (*A. richardii* on Grenada and *A. bimaculatus* on St. Eustatius) tended to perch higher than its smaller sympatric congener.

Niche breadths are widest in areas that provide the greatest diversity in structural habitats, supporting our initial predictions that ecologically versatile Lesser Antillean anoles would adjust readily to available resources. This is similar to conclusions previously reported by Eaton et al. (2002), Harris et al. (2004), and Medina Díaz et al. (2005), who used similar methods in studies of Anguillian, Grenadian, and St. Eustatian anoles, respectively.

The lowest niche overlaps based on perch heights were between adult male *A. griseus*, which perched higher than all other size classes of either species. The highest overlap values based on perch diameters were between juvenile *A. griseus* and adult *A. trinitatis*, which tended to share the bases of large trunks, whereas juvenile *A. trinitatis* were more likely to use smaller woody and herbaceous plants. These data also correspond closely to those for Grenadian (Harris et al. 2004) and St. Eustatian (Medina Díaz et al. 2005) anoles, where the larger species dominated perches on larger trees, although both Grenadian species appeared to prefer larger trees when available, whereas the smaller St. Eustatian species (*A. schwartzi*) was more closely associated with terrestrial and saxicolous perches and herbaceous vegetation.

We saw few *A. trinitatis* and no *A. griseus* in direct sunlight. In a concurrent study, M. A. Powell (pers. comm.) noted that, even in the early morning hours, anoles were not seen basking in direct sunlight, moving directly from sleeping sites to shaded areas. This differs from previously published observations (e.g., Powell 1999),

which described basking behavior (oriented up), especially during morning hours. However, by mid-morning and during the afternoon, when we sampled sites, temperatures were high and the use of partially to fully shaded perches was predictable (e.g., Eaton et al. 2002; Harris et al. 2004; Medina Díaz et al. 2005). On Grenada, *A. richardii* appeared to prefer less insolated situations than *A. aeneus* (Harris et al. 2004), whereas *A. bimaculatus* on St. Eustatius was considerably more tolerant of open habitats than *A. schwartzi* (Medina Díaz et al. 2005).

An underlying assumption regarding sympatric island populations of anoles is that they partition resources by differing in size and resource use (e.g., Rand and Williams 1969; Beuttell and Losos 1999), with anoles on two-species Lesser Antillean islands almost invariably differing in sizes (an exception is *A. gingivinus* and *A. pogus* on St. Martin/St. Maarten) and habitat preferences (e.g., Roughgarden et al. 1983; Roughgarden 1995; Buckley and Roughgarden 2005). In particular, Buckley and Roughgarden (2005) indicated that anoles partition local habitat along perch-height and microclimate axes. They further indicated that sympatric anoles in the northern Lesser Antilles partition local habitats by perch height and have overlapping distributions at the landscape scale, whereas sympatric anoles in the southern Lesser Antilles partition local habitats by microclimate and specialize in particular habitats at the landscape scale. In both the north and south, they suggested that species use different perch heights and microclimates only in areas of species overlap along an elevational gradient.

Our data and those using essentially the same methods on other two-species Lesser Antillean islands (Harris et al. 2004; Medina Díaz et al. 2005) generally support the contentions of Buckley and Roughgarden (2005) in that size differences and habitat preferences of the two species did affect relative abundances and at least some aspects of structural habitat use (e.g., absence of *A. griseus* from drier, more intensely insolated sites). However, structural habitat use and microclimatic preferences are anything but rigidly defined, reaffirming con-

tentions that Lesser Antillean anoles (and Lesser Antillean reptiles in general) are ecologically versatile (Henderson and Powell 1999, 2001; Eaton et al. 2002; Harris et al. 2004; Medina Díaz et al. 2005; Powell and Henderson 2005). Overlap among at least some size classes of both species and numerous observations of individuals of different species perched side-by-side suggest that general patterns of niche partitioning do not apply in all instances and can vary considerably under some circumstances.

*Acknowledgments.*—Christopher S. Mallery, Jr., Martha A. Marcum, and David S. Steinberg provided invaluable assistance with painting lizards and data entry. Mike L. Treglia and John S. Parmerlee, Jr. provided technical support. This manuscript benefited considerably from comments by Robert W. Henderson and John S. Parmerlee, Jr. Permits to conduct research on St. Vincent were issued by the Department of Forestry, St. Vincent and the Grenadines. Brian Johnson, Director, Cornelius Richards, Amos Glasgow, and especially FitzGerald Providence facilitated our efforts on St. Vincent. Dennis Ambrose and the Horne family graciously allowed us to work on their properties at Akers and Bambareaux, respectively. Fieldwork was funded by a grant from the National Science Foundation (USA) to Robert Powell (DBI-0242589).

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