

B R E V I O R A

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS.

8 OCTOBER 2010

NUMBER 520

THE ANOLES OF SOROA: ASPECTS OF THEIR ECOLOGICAL RELATIONSHIPS

LOURDES RODRÍGUEZ SCHETTINO,¹ JONATHAN B. LOSOS,² PAUL E. HERTZ,³ KEVIN DE QUEIROZ,⁴ ADA R. CHAMIZO,¹ MANUEL LEAL,⁵ AND VILMA RIVALTA GONZÁLEZ¹

ABSTRACT. Most lizard communities are characterized by having one or two dominant species and a handful of other species that occur at relatively low densities. However, Soroa, a site in the Sierra del Rosario of western Cuba, is home to 11 sympatric species of *Anolis*, of which nine are found in high abundance. In this study, we evaluate how interspecific differences in structural niche, thermal niche, body size, and behavior might allow the extraordinarily high anole species diversity at this site. We found that all pairs of species differ in at least one of the following niche axes: vegetation types occupied, substrates used, perch height, irradiance at occupied perch sites, and body temperature. Interspecific differences across these axes might serve to reduce competition, allowing the 11 species to live sympatrically within a relatively small geographic area.

KEY WORDS: *Anolis*; Cuba; Soroa; community structure

INTRODUCTION

In their pioneering 1969 paper “The anoles of La Palma: Aspects of their ecological relationships,” Rand and Williams described how seven sympatric *Anolis* species partition habitat in the Cordillera Central of the Dominican Republic. Following earlier work by Rand (1964, 1967) and Schoener (1967, 1968), Rand and Williams examined the

structural and climatic habitats of the seven species. They also introduced a classification of structural habitat use, dividing the species into six categories that reflected where adult males engage in most of their activities: crown anoles, twig anoles, trunk-crown anoles, trunk anoles, trunk-ground anoles, and grass-bush anoles. Recognition of these ecological differences soon led Williams to

¹ Instituto de Ecología y Sistemática, CITMA, La Habana, Cuba; e-mail: zoologia.ies@ama.cu

² Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, U.S.A.; e-mail: jllosos@oeb.harvard.edu

³ Department of Biological Sciences, Barnard College, New York, New York, U.S.A.; e-mail: phertz@barnard.edu

⁴ National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.; e-mail: dequeirozk@si.edu

⁵ Duke University, Durham, North Carolina, U.S.A.; e-mail: mleal@duke.edu

propose the ecomorph concept: the idea that species within a community adapt morphologically and behaviorally to using different parts of the habitat and that, across communities, similar sets of habitat specialists evolve repeatedly (Williams, 1972, 1983). Although resource partitioning and the evolution of convergent ecomorphs have been examined in great detail for three of the four islands in the Greater Antilles, our knowledge of *Anolis* communities in Cuba has, until recently, been scant (Williams, 1972, 1983; see review in Losos, 2009). Our goal in this paper is to provide a description of the diverse anole fauna at a locality in the Sierra del Rosario, near the town of Soroa in western Cuba, from the perspective that Rand and Williams developed. Rand and Williams actually visited Soroa in October 1981 and June 1983—in the company of Lourdes Rodríguez Schettino, Julio Novo, Dale Marcellini, Noel Gonzalez, and Alberto Coy Otero—and drafted a partial manuscript that was never completed. We include a copy of this manuscript as online supplementary material.

Here, we report on parts of the lizard community at Soroa, which includes 25 lizard species, 24 of which are diurnal (Rodríguez Schettino *et al.*, 2005). Remarkably, 11 of these species belong to the clade *Anolis*; we include within *Anolis* the subclade *Chamaeleolis* (Hass *et al.*, 1993; Jackman *et al.*, 1999), which has traditionally been treated as a separate genus (e.g., Williams, 1976). Thus, at the time we conducted our study, Soroa was home to the highest diversity of anoles yet discovered. More recently, Diaz *et al.* (1998) and Garrido and Hedges (2001) have described sites in eastern Cuba that house 15 and 14 anole species, respectively; some sites in Central America might be equally species rich (Losos, 2009). To date, however, none of these communities has received detailed ecological study.

The literature on resource partitioning in tropical lizard communities suggests that the use of different perch sites and microhabitats with different irradiance and thermal properties often allows sympatric species to avoid intense interspecific competition (Schoener and Gorman, 1968; Schoener, 1977; Heatwole, 1982; Williams, 1983; Jenssen *et al.*, 1988; Hertz, 1991; Losos, 1992; Powell *et al.*, 1996; Leal and Fleishman, 2002). Martínez Reyes (1995) found 11 anole species at Soroa and noted that most of them perched on tree trunks or shrubs. In a field trip undertaken in May and June 1997, the authors of the current contribution collected data on the type, height, and diameter of the perches selected for all 11 species in early summer. After subjecting these data to a principal components analysis, we published a short paper on niche lability in this lizard community (Losos *et al.*, 2003). However, neither of the aforementioned contributions presented the raw data on which the analyses were based. In the current paper, we provide qualitative and quantitative descriptions of the natural history and habitat use of the anole species at Soroa to characterize more thoroughly the composition and structure of the community. Our observations should be useful as baseline data for detecting potential changes in the natural history of these species as climate change over the coming decades alters the environment they occupy (Rodríguez Schettino and Rivalta González, 2007; Huey *et al.*, 2009).

MATERIALS AND METHODS

The locality we identify as Soroa encompasses the grounds of the Horizontes Hotel and the forested area at 700–800 m elevation adjacent to a pathway along the Manantiales River, ending at the Arco Iris waterfall. It is located at 22°48'5"N, 83°0'53"W (WGS84) near the western limit of the Biosphere Reserve “Sierra del Rosario” in the eastern-

most part of the Cordillera de Guaniguanico, Pinar del Río province, Cuba. Soroa has the highest species richness of vertebrates of any locality in the Reserve, mainly in the evergreen and gallery forests (Rodríguez Schettino *et al.*, 1999).

Macrohabitat Types

Because Soroa is an actively used resort, the site includes buildings, shrubby “living fences,” chain-link fencing supported by metal posts, and various other human constructions (largely concrete) that some *Anolis* species use as perch sites. The study site also includes a modest patch of evenly planted Ocuje trees (*Calophyllum antillarum*), as well as the three following natural vegetation types described by Capote (1989).

Evergreen forest. The canopy layer has trees 20–30 m tall. The most abundant species are *Erythrina poeppigiana* (búcare), *Zanthoxylum martinicense* (ayúa), *Prunus occidentalis* (cuajani), *Hibiscus elatus* (majagua), *C. antillarum* (ocuje), *Ficus aurea* (jagüey), *Cedrela odorata* (cedro), *Bursera simaruba* (almácigo), *Pseudolmedia spuria* (macagua), *Oxandra lanceolata* (yaya), *Matayba apetala* (macurije), *Roystonea regia* (palma royal), and *Syzygium jambos* (pomarossa). The understory layer is 3–5 m in height; the most abundant understory species are *Piper aduncum* (platanillo de Cuba) and *Psychotria horizontalis* (dagame cimarrón).

Gallery forest. The canopy layer has trees of 15–20 m, with many lianas and grasses; the most abundant species are *S. jambos* (pomarossa), *C. antillarum* (ocuje), *Lonchocarpus dominguensis* (guamá), and *R. regia* (palma royal).

Secondary vegetation. There are canopy, understory, and grass layers with many individuals of *H. elatus* (majagua), *R. regia* (palma royal), *Cecropia peltata* (yagruma), *Muntingia calabura* (capulí), *Z. martinicense* (ayúa), and *Solanum umbellatum* (pendejera).

Lizard Surveys

During our surveys, we searched for lizards by walking slowly through disturbed habitats adjacent to the hotel (buildings, fences, and a planted woodland) and through a nearby forested area (from the head of the trail across the road from the hotel to the waterfall at the bottom of that trail). We sampled lizards in whatever habitats they occupied; for some species, we report data separately for lizards that occupied natural habitats and those that lived on or around human constructions. Whenever possible, we report data on males and females separately; however, it was not always possible to identify the sex of individual *Anolis barbatus* and *Anolis luteogularis* observed from a distance because these species exhibit little sexual size dimorphism and because both males and females have large dewlaps.

All observations were made between 0800 and 1800 hours over 19 days (May 21 to June 8, 1997). Because previous studies of West Indian anoles have shown that perch sites and sun/shade conditions are the resource axes that sympatric species most commonly partition (e.g., Rand, 1964; Schoener, 1974; Roughgarden *et al.*, 1981), during each excursion, we collected data on the location where each lizard was first spotted, including the type of substrate (trunk, branch [including twigs], leaf, vine, rock, ground, or artificial substrate), the height above ground, the diameter of the substrate (no measurement for ground, walls, or leaves), and the light conditions (full sun, full shade, or filtered sun). Lizards that were moving in response to our presence when first sighted were excluded. Some lizards were captured to obtain their body temperatures with a quick-reading electronic thermocouple thermometer (0.1°C resolution). We measured activity by walking transects at 1.5-h intervals throughout 2 days and noting every lizard observed within the forest, as well as in

disturbed habitats (planted ocuje trees, living fence, and chain-link fence). For species that we saw only rarely, the time of activity data were augmented with observations made on other days; in some cases, the precise time of observation was not recorded, and some data were allotted equally to two adjacent time periods if they were recorded as exactly the minute separating the periods. Whenever we captured a lizard to record its body temperature, we also measured its snout–vent length (SVL). Losos *et al.* (2003) provides a more comprehensive description of the methods used for these surveys.

We report the frequencies with which lizards used different substrates (listed above), as well as the frequencies at which they perched in full sun, filtered sun, or full shade during sunny weather. We also report descriptive statistics for perch heights and diameters, body temperatures, and SVLs of lizards sampled.

Behavioral Observations

We located adult male anoles by walking slowly through the habitat until we found an apparently undisturbed lizard. Animals were watched for up to 20 minutes, although some moved out of sight before the observation period ended. We used data only from individuals that we observed for at least 5 minutes and that moved at least five times, following our previous methods (Losos, 1990). We calculated moves per minute as the number of individual movements divided by time. Moves were classified as jumps, runs, or walks. To be consistent with previous studies (e.g., Losos, 1990), data from only one observer (JBL) were used to distinguish between runs and walks. For that reason, percentage of jumps is calculated on the basis of larger sample sizes than the other two measures, and the frequencies of the three movement types do not sum to 1.0. Percent displaying is the percentage of time a lizard was dewlapping,

head bobbing, or performing some other social display behavior. Data for *A. barbatus* are taken from Leal and Losos (2000); these data were collected for both males and females, including some subadults, and do not include information on moves per minute.

RESULTS

Body Size

The 11 anole species at Soroa vary greatly in body size (Table 1). Two species—*A. angusticeps* and *A. alutaceus*—are notably smaller than most (mean adult male SVL < 45 mm). Most species are of intermediate size (mean adult male SVL = 50–70 mm). Three species—*A. barbatus*, *A. luteogularis*, and *A. vermiculatus*—are substantially larger than the others (mean adult male SVL > 100 mm). In most species, males appear to be larger than females, but our sample sizes for some species and sex combinations are too small to allow firm conclusions. The trunk-ground species *A. homolechis* and *A. sagrei* exhibit essentially no differences in body size among sites.

Macrohabitat Distribution

Some of the 11 *Anolis* species at Soroa exhibit substantial differences in the macrohabitats and forest vegetation types that they occupy (Table 2). Five species (*A. allogus*, *A. angusticeps*, *A. barbatus*, *A. homolechis*, and *A. luteogularis*) occur in all three forest types; two species (*A. porcatus* and *A. sagrei*) occupy two forest types; and four species (*A. alutaceus*, *A. loysianus*, *A. mestrei*, and *A. vermiculatus*) are restricted to just one forest type.

Taking into account all the macrohabitats available at Soroa (Table 2), *A. homolechis* is the most widely distributed species, occurring in disturbed habitats (e.g., the planted woodlands and living fences) and open forest edges; however, it does not occupy chain-link fencing (not distinguished as a separate category in

TABLE 1. SNOUT-VENT LENGTH (SVL) OF 11 *ANOLIS* SPECIES FROM SOROA BY SITE AND SEX. LIZARDS WERE MEASURED AT THE MOMENT OF CAPTURE.

<i>Anolis</i> Species	Site	SVL (mm)					
		Males			Females		
		N	Mean	SD	Range	N	Mean
<i>A. alutaceus</i>	Forest	3	39.7	7.37	34–48	1	33
<i>A. angusticeps</i>	Forest	—				4	35.2
<i>A. loysianus</i>	Forest	5	42.8	5.23	40–52	—	
<i>A. sagrei</i>	Chain-link fence	24	50.6	4.35	34–55	5	41.6
	Living fence	15	50.4	4.29	40–56	—	
	All	39	50.5	4.27	34–56	5	41.6
<i>A. mestrei</i>	Forest	52	52.0	4.08	40–60	22	41.6
<i>A. allogus</i>	Forest	86	52.5	6.70	34–62	20	42.0
<i>A. homolechis</i>	Forest	49	52.0	3.42	45–60	33	41.4
	Living fence	22	52.2	2.20	48–55	4	42.3
	Planted woodland	26	51.8	2.30	48–56	3	43.7
	All	97	52.0	2.88	45–60	40	41.7
<i>A. porcatus</i>	Forest	2	67.2	11.70	59–76	—	
<i>A. barbatus</i>	Forest	3	106.7	20.50	83–119	2	131.0
<i>A. luteogularis</i>	Forest	1	183.0			6	154.7
<i>A. vermiculatus</i>	Forest	11	121.5	5.56	116–128	13	78.3
							6.83
							70–90

Table 2), the most exposed habitat available at Soroa. *Anolis luteogularis* and *A. porcatus* have similarly broad habitat distributions (five macrohabitats each), but the former species only rarely occurs on or around human constructions, whereas the latter species is abundant in that habitat. *Anolis sagrei* occupies fairly sunny areas of the forest, and it is abundant on living fences and human con-

structions. Four species (*A. alutaceus*, *A. loysianus*, *A. mestrei*, and *A. vermiculatus*) have the narrowest habitat distributions, each being restricted to just one (forested) habitat type.

Structural Habitats

The anole species at Soroa can be divided into two groups on the basis of mean perch

TABLE 2. MACROHABITAT DISTRIBUTIONS OF 11 *ANOLIS* SPECIES AT SOROA. FOREST VEGETATION TYPES FOLLOW CAPOTE (1989).

<i>Anolis</i> Species	Forest Vegetation						
	Evergreen	Gallery	Secondary	Planted	Woodland	Living Fences	Artificial Structures
<i>A. allogus</i>	X	X	X				
<i>A. alutaceus</i>							X
<i>A. angusticeps</i>	X	X	X				
<i>A. barbatus</i>	X	X	X				
<i>A. homolechis</i>	X	X	X	X		X	X
<i>A. loysianus</i>	X						
<i>A. luteogularis</i>	X	X	X	X		X	
<i>A. mestrei</i>		X					
<i>A. porcatus</i>		X	X	X		X	X
<i>A. sagrei</i>	X	X	X			X	X
<i>A. vermiculatus</i>	X						

TABLE 3. FREQUENCIES OF SUBSTRATE USE BY 11 *ANOLIS* SPECIES AT SOROA. DATA FOR MALES AND FEMALES OF *A. LUTEOGULARIS* AND *A. BARBATUS* ARE COMBINED BECAUSE IT IS NOT POSSIBLE TO DETERMINE THEIR SEX AT A DISTANCE.

<i>Anolis</i> Species	N	Frequency						
		Trunk	Branch	Leaf	Vine	Rock	Ground	Artificial
Lizards sampled in natural areas								
<i>A. allogus</i> ♂	139	0.56	0.08		0.04	0.25	0.04	0.04
<i>A. allogus</i> ♀	20	0.45	0.15		0.10	0.10	0.10	0.10
<i>A. alutaceus</i> ♂	23	0.22	0.35	0.17	0.13	0.13		
<i>A. alutaceus</i> ♀	8	0.25	0.26	0.13	0.13	0.25		
<i>A. angusticeps</i> ♂	4	0.50	0.50					
<i>A. angusticeps</i> ♀	8	0.38	0.50		0.13			
<i>A. barbatus</i>	9	0.56	0.44					
<i>A. homolechis</i> ♂	83	0.52	0.19		0.01	0.12	0.07	0.08
<i>A. homolechis</i> ♀	36	0.39	0.17		0.06	0.11	0.14	0.14
<i>A. loysianus</i> ♂	11	0.91	0.09					
<i>A. loysianus</i> ♀	5	1.00						
<i>A. luteogularis</i>	28	0.39	0.39	0.04	0.11	0.04		0.04
<i>A. mestrei</i> ♂	96	0.25	0.08		0.07	0.50	0.05	0.04
<i>A. mestrei</i> ♀	22	0.14	0.09			0.68		0.09
<i>A. porcatus</i> ♂	8	0.38	0.38	0.25				
<i>A. porcatus</i> ♀	6	0.83		0.17				
<i>A. sagrei</i> ♂	45	0.18	0.07	0.02		0.07		0.67
<i>A. sagrei</i> ♀	5	0.40						0.60
<i>A. vermiculatus</i> ♂	18	0.44	0.22			0.28		0.06
<i>A. vermiculatus</i> ♀	17	0.12	0.06			0.71	0.12	
Lizards sampled around human constructions								
<i>A. homolechis</i> ♂	79	0.27	0.03	0.01		0.04		0.66
<i>A. homolechis</i> ♀	36	0.25				0.03	0.03	0.69
<i>A. porcatus</i> ♂	13	0.62	0.08	0.15				0.15
<i>A. porcatus</i> ♀	6		0.17	0.67	0.17			
<i>A. sagrei</i> ♂	44	0.09	0.05	0.02		0.07	0.02	0.75
<i>A. sagrei</i> ♀	7		0.28			0.14		0.57

heights of males (Tables 3, 4a): those that perch closer to the ground (on average, < 2 m) and those that perch higher in the vegetation (on average, ≥ 3 m). Perch heights of females are similar to those of males in some species, but quite different in others (Table 4a).

Three species that use lower perches—*A. allogus*, *A. homolechis*, and *A. mestrei*—tend to use broad natural surfaces, such as tree trunks or rock walls; *A. mestrei*, in particular, is always found on or near rock walls in the forest. *Anolis sagrei*, a trunk-ground anole like the other three, frequently perches on human constructions, primarily walls or

fences. Another species found low to the ground is *A. alutaceus*, which usually perches on narrow vegetation, including thin branches, vines, and ferns. *Anolis vermiculatus* was almost invariably found within 5 m of streams (maximum reported distance is 15 m; Rodríguez Schettino *et al.*, 1987), often perching as high as 4 m on trunks, on branches that hung over the water, or on rocks or walls along the streamside.

The remaining species were normally found higher in the vegetation, at or above 3 m. Four species (*A. angusticeps*, *A. loysianus*, *A. barbatus*, and *A. luteogularis*)

TABLE 4A. PERCH HEIGHTS FOR 11 *ANOLIS* SPECIES AT SOROA. SPECIES ARE LISTED IN ASCENDING ORDER OF MEAN PERCH HEIGHTS OF MALES. DATA FOR MALE AND FEMALE *A. LUTEOGULARIS* ARE COMBINED BECAUSE THE SEXES CANNOT BE DISTINGUISHED FROM A DISTANCE. DATA FOR *A. BARBATUS* ARE FROM SIX INDIVIDUALS, SOME OF WHICH PROBABLY WERE SUBADULTS, AND REPRESENT THE MEAN OF THE MIDDLE OF THE HEIGHT RANGES USED BY EACH INDIVIDUAL (DATA FROM LEAL AND LOSOS, 2000); RANGES ARE THE LOWEST AND HIGHEST POINT ACROSS ALL INDIVIDUALS. GIVEN THE COMPOSITE NATURE OF THESE VALUES, NO STANDARD DEVIATIONS ARE REPORTED.

<i>Anolis</i> Species	Perch Diameter (mm)							
	Males				Females			
	N	Mean	SD	Range	N	Mean	SD	Range
Lizards sampled in natural areas								
<i>A. sagrei</i>	46	0.9	0.4	0.2–1.9	5	0.9	0.6	0.3–1.8
<i>A. allogus</i>	139	1.0	0.6	0.0–3.0	16	0.5	0.4	0.1–1.5
<i>A. mestrei</i>	93	1.4	1.1	0.0–7.0	21	0.8	0.9	0.0–4.0
<i>A. homolechis</i>	84	1.5	2.4	0.0–17.0	23	0.6	0.5	0.1–2.5
<i>A. alutaceus</i>	35	1.5	1.1	0.2–5.0	10	2.2	1.9	0.3–6.0
<i>A. vermiculatus</i>	17	1.6	1.3	0.0–4.0	10	0.5	0.7	0.0–1.5
<i>A. barbatus</i>	3	2.8	—	0.5–4.0	3	5.2	—	0.3–19
<i>A. loysianus</i>	11	3.1	1.5	1.1–5.0	6	1.6	1.1	0.3–3.0
<i>A. luteogularis</i> (♂ + ♀)	28	5.9	5.1	0.3–20.0				
<i>A. angusticeps</i>	3	6.3	3.8	2.0–9.0	9	2.2	1	1.0–4.0
<i>A. porcatus</i>	8	12.0	9.7	3.0–30.0	7	7.0	4.7	1.0–14.0
Lizards sampled around human constructions								
<i>A. homolechis</i>	158	1.0	0.8	0.1–9.0	55	0.6	0.4	0.0–1.5
<i>A. sagrei</i>	88	1.0	0.6	0.0–1.8	23	0.5	0.6	0.0–1.8
<i>A. porcatus</i>	13	2.0	1.1	1.0–5.0	6	2.4	1.4	1.5–5.0

spend most of their time on trunks, branches, or both in the subcanopy and canopy. *Anolis porcatus*, which frequently perches on trunks and branches and occasionally on leaves, occupies substantially higher perches in the forest, often near the canopy, than it does around human constructions. By contrast, we found *A. angusticeps* primarily on branches, whereas *A. barbatus* occupies trunks and branches with nearly equal frequency. With regard to the diameter of the perches used, the average size of substrates used by most species was moderate (in the range of 10–18 cm; Table 4b). Two species, *A. alutaceus* and *A. barbatus*, used much narrower supports; *A. mestrei* also used narrow perches when it perched on vegetation. Surprisingly, *A. angusticeps*, commonly categorized as a twig anole (Irschick and Losos 1996), used relatively

large supports on average, although it was sometimes seen on narrow surfaces (discussed further below). The three species that were commonly observed in both natural areas and around human constructions used similar perches in both areas.

Climatic Habitat and Body Temperatures

The 11 *Anolis* species at Soroa also differ in their use of perch sites in full sun, filtered sun, or shade (Table 5). Within the forest, six species (*A. alutaceus*, *A. angusticeps*, *A. barbatus*, *A. loysianus*, *A. luteogularis*, and *A. mestrei*) perched primarily in fully shaded microhabitats (> 60% of observations). The remaining species used a more even mix of sunny and shaded perch sites. Notably, only one species, *A. porcatus*, spent a majority of its time perched in full sun. All three species that we routinely sampled in the warmer

TABLE 4B. DIAMETERS OF PERCHES (ROCK AND GROUND PERCHES EXCLUDED) USED BY 11 *ANOLIS* SPECIES AT SOROA. SPECIES LISTED AS IN TABLE 4A. DATA FOR MALE AND FEMALE *A. LUTEOGULARIS* ARE COMBINED BECAUSE THE SEXES CANNOT BE DISTINGUISHED FROM A DISTANCE. DATA FOR *A. BARBATUS* ARE FROM SIX INDIVIDUALS, SOME OF WHICH PROBABLY WERE SUBADULTS AND REPRESENT ALL SURFACES USED DURING BEHAVIORAL OBSERVATIONS; THE SAMPLE SIZES REPORTED ARE NUMBER OF OBSERVATIONS, NOT NUMBER OF INDIVIDUALS (DATA FROM LEAL AND LOSOS [2000]; NO STANDARD DEVIATION BECAUSE THE VALUES ARE BASED ON WEIGHTED MEANS FOR INDIVIDUALS). SAMPLE SIZES FOR DIAMETER ARE LOWER THAN FOR PERCH HEIGHT BECAUSE DIAMETER WAS NOT RECORDED FOR LIZARDS ON THE GROUND, ON WALLS, OR ON LEAVES.

<i>Anolis</i> Species	Perch Diameter (mm)							
	Males				Females			
	N	Mean	SD	Range	N	Mean	SD	Range
Lizards sampled in natural areas								
<i>A. sagrei</i>	37	6.2	4.5	0.2–20	4	6.3	7.1	0.2–16
<i>A. allogus</i>	139	11.4	13.9	0.5–80	13	10.0	12.7	0.4–39
<i>A. mestrei</i>	40	1.0	12.9	1.0–50	5	11.0	7.6	2.5–22
<i>A. homolechis</i>	64	12.1	13.2	0.6–70	26	10.9	13.4	0.7–60
<i>A. alutaceus</i>	28	1.1	1.4	0.2–7.0	7	2.1	2.8	0.3–8.0
<i>A. vermiculatus</i>	12	14.6	17.5	1.5–67	3	10.0	13.0	2.0–25
<i>A. barbatus</i>	27	1.7	—	0.5–4.0	27	2.0	—	0.3–19
<i>A. loysianus</i>	11	18.7	14.7	2.0–50	6	27.5	20.7	8–60
<i>A. luteogularis</i> (♂ + ♀)	32	12.5	12.7	1.0–50				
<i>A. angusticeps</i>	4	10.6	9.9	2.5–25	9	14.1	12.0	0.8–30
<i>A. porcatus</i>	7	11.4	9.7	1.0–20	7	14.6	10.6	5.0–33
Lizards sampled around human constructions								
<i>A. homolechis</i>	149	15.8	9.4	1.3–60	52	13.1	6.8	1.3–30
<i>A. sagrei</i>	76	6.6	4.8	0.5–25	11	5.0	4.2	0.5–15
<i>A. porcatus</i>	9	11.9	11.3	1.5–40	4	6.6	5.6	0.5–14.0

habitats around human constructions (*A. homolechis*, *A. porcatus*, and *A. sagrei*) used a mixture of sunny and shaded perch sites.

Mean body temperatures divide the 11 species into three groupings that reflect their macrohabitat preferences and their structural and thermal niches (Table 6). Among the species sampled in natural areas, only *A. sagrei* exhibited mean body temperatures > 30°C; three species (*A. allogus*, *A. barbatus*, and *A. mestrei*) had mean body temperatures < 28°C; and six species (*A. alutaceus*, *A. angusticeps*, *A. homolechis*, *A. loysianus*, *A. luteogularis*, and *A. vermiculatus*) exhibited mean body temperatures within a narrow intermediate range (28.7–29.6°C).

Among the three species sampled around human constructions, mean body temperatures were slightly lower than those recorded in

natural areas for *A. homolechis* and *A. sagrei*; *A. porcatus*, which was not sampled in the forest, had a very high mean body temperature.

Activity Times

Activity times varied among species in concert with their thermal biology (Table 7). Among the four trunk-ground anoles in the forest, the two shade-dwelling species with low body temperatures (*A. allogus* and *A. mestrei*) were most active from early morning through midafternoon. By contrast, the heliothermic species with high body temperature (*A. sagrei*) was most active from midday through late afternoon, and the most broadly distributed species (*A. homolechis*) exhibited a fairly consistent level of activity from early morning until sundown. For most of the other forest-dwelling species, activity also peaked in midafternoon.

TABLE 5. FREQUENCY AT WHICH 11 *ANOLIS* SPECIES AT SOROA PERCHED IN SUN, FILTERED SUN, OR SHADE DURING SUNNY WEATHER. DATA FOR MALE AND FEMALE *A. LUTEOGULARIS* AND *A. BARBATUS* ARE COMBINED BECAUSE THE SEXES CANNOT BE DISTINGUISHED FROM A DISTANCE.

<i>Anolis</i> Species	Frequency							
	Males				Females			
	N	Full Shade	Filtered Sun	Full Sun	N	Full Shade	Filtered Sun	Full Sun
Lizards sampled in natural areas								
<i>A. allogus</i>	65	0.43	0.43	0.14	9	0.56	0.33	0.11
<i>A. alutaceus</i>	12	1.00			3	0.33	0.33	0.33
<i>A. angusticeps</i>	1			1.00	5	0.80		0.20
<i>A. barbatus</i>	6	0.83		0.17				
<i>A. homolechis</i>	52	0.21	0.33	0.46	20	0.35	0.30	0.35
<i>A. loysianus</i>	9	0.67	0.22	0.11	4	1.00		
<i>A. luteogularis</i>	19	0.63	0.26	0.11				
<i>A. mestrei</i>	79	0.66	0.23	0.11	16	0.69	0.31	
<i>A. porcatus</i>	3	0.33		0.67	3		0.33	0.67
<i>A. sagrei</i>	38	0.58	0.03	0.40	2		1.00	
<i>A. vermiculatus</i>	12	0.17	0.58	0.25	17	0.24	0.59	0.18
Lizards sampled around human constructions								
<i>A. homolechis</i>	94	0.37	0.39	0.23	17	0.53	0.35	0.12
<i>A. porcatus</i>	9	0.78		0.22	4		0.25	0.75
<i>A. sagrei</i>	41	0.42	0.44	0.15	6	0.33	0.67	

In the areas sampled outside the forest, both species that occupy open habitats (*A. porcatus* and *A. sagrei*) were active in the morning, an unsurprising result, given that these habitats heat up much earlier in the day and reach higher temperatures than do locations within the forest. By contrast, *A. homolechis* showed high levels of activity over a narrower range of times (midday) than it does in the forest.

Behavior

The species varied fivefold in their rates of movement (Table 8). The more terrestrial species tended to be relatively inactive, whereas some of the more arboreal species (*A. angusticeps*, *A. loysianus*, and *A. porcatus*) moved at much higher rates, observations that parallel those seen for anoles on other islands in the Greater Antilles (Johnson *et al.*, 2008). *Anolis alutaceus* jumped twice as much as any other species. Trunk-ground anoles (*A.*

allogus, *A. homolechis*, *A. mestrei*, and *A. sagrei*) and *A. loysianus* tended to run more than other species, whereas the twig (*A. angusticeps*) and large arboreal species (*A. luteogularis*), as well as *A. alutaceus*, ran relatively infrequently. *Anolis angusticeps* and *A. barbatus* walked considerably more often than other species. Percentage of time spent displaying also varied greatly among species, with trunk-ground anoles, *A. barbatus*, and *A. loysianus* displaying more frequently than other species.

Complementarity of Resource Use among Species

At Soroa, species that are ecologically similar in one niche dimension often differ in another. For example, *A. allogus* and *A. homolechis* perch low on trunks (Table 4a) in all three types of forest vegetation (Table 2). Although they are similar in size (Table 1)

TABLE 6. BODY TEMPERATURES FOR 11 *ANOLIS* SPECIES AT SOROA. SPECIES ARE LISTED IN DESCENDING ORDER OF MALE MEAN BODY TEMPERATURES.

<i>Anolis</i> Species	Body Temperature (°C)							
	Males				Females			
	N	Mean	SD	Range	N	Mean	SD	Range
Lizards sampled in natural areas								
<i>A. sagrei</i>	9	32.1	1.8	29.6–34.9	5	32.9	1.8	31.6–33.9
<i>A. vermiculatus</i>	7	29.6	1.7	26.7–32.0	9	29.8	1.8	27.0–32.1
<i>A. luteogularis</i>	8	29.4	1.1	28.0–30.7	—	—	—	—
<i>A. loysianus</i>	3	29.3	1.6	27.7–30.8	2	28.6	0.3	28.4–28.8
<i>A. angusticeps</i>	—	—	—	—	3	29.2	0.4	28.7–29.4
<i>A. homolechis</i>	51	29.2	2.4	24.2–33.5	34	28.7	2.5	22.3–33.4
<i>A. alutaceus</i>	4	28.7	1.3	27.6–30.6	3	29.1	1.0	28.0–29.9
<i>A. mestrei</i>	53	27.5	1.9	22.8–30.8	23	27.6	2.0	22.1–29.9
<i>A. barbatus</i>	3	27.3	0.2	27.1–27.5	—	—	—	—
<i>A. allegus</i>	82	26.9	2.2	21.3–31.1	18	26.9	1.9	24.2–29.9
Lizards sampled around human constructions								
<i>A. porcatus</i>	3	32.7	2.19	30.8–35.1	7	31.5	1.4	29.8–33.3
<i>A. sagrei</i>	87	30.4	3.36	24.5–36.8	16	28.2	2.1	24.4–30.9
<i>A. homolechis</i>	133	28.5	2.02	24.1–32.5	54	27.6	2.1	24.6–32.7

and exhibit similar patterns of substrate use (Table 3), *A. homolechis* occupies sunnier areas of the forest (Table 5), and this behavioral difference is reflected in a difference in their mean body temperatures (Table 6). A third species, *A. mestrei*, which is similar in size and habitus to the other two, also perches low in the gallery forest, but it frequently uses rock faces, which differentiates it ecologically from the other two species. Finally, *A. sagrei*, which is similar in size and closely related to the three aforementioned species, uses similar perch heights and substrates, but it is most abundant in nonforested habitats, and its mean body temperature is among the highest of all the anoles we sampled at Soroa.

A different pattern of ecological differentiation is seen among the three species that occupy high, relatively narrow perches within the forest (*A. angusticeps*, *A. barbatus*, and *A. luteogularis*): *A. angusticeps* is much smaller than the other two species, which

also differ substantially in size; these differences in SVL almost certainly enable the species to consume different foods (Schoener 1967). Indeed, we observed only *A. luteogularis* feeding on smaller species of anoles.

NATURAL HISTORY OF SOROA ANOLES

In this section we briefly describe our natural history observations on the 11 *Anolis* species at Soroa. These descriptions include information about the colors of their dewlaps because previous research has established that the diversity of *Anolis* dewlap patterns and behavioral displays, as well as redundancy in dewlap information content, allows them to communicate species identity unambiguously (Rand and Williams 1970; Losos and Chu 1998; Nicholson *et al.* 2007). Our observations of syntopic species (e.g., the four trunk-ground anoles) at Soroa are consistent with this hypothesis. All photographs are males and, except where noted, from Soroa.

TABLE 7. RELATIVE ACTIVITY TIMES FOR 11 *ANOLIS* SPECIES AT SOROA. FOR EACH SPECIES, ENTRIES IN THE TABLE RECORD THE PERCENTAGE OF ALL LIZARDS OBSERVED (N) THAT WERE SPOTTED DURING EACH OF EIGHT TIME PERIODS. CENSUS DATA WERE COLLECTED WHILE WALKING TRANSECTS ON EACH OF TWO DAYS. DATA WERE AUGMENTED BY OBSERVATIONS MADE ON OTHER DAYS FOR SPECIES LESS COMMONLY SEEN; FOR THESE OBSERVATIONS, SOME POINTS WERE ALLOTTED EQUALLY TO TWO ADJACENT TIME PERIODS IF THEY WERE RECORDED AS EXACTLY THE MINUTE SEPARATING THE PERIODS.

<i>Anolis</i> Species	N	Relative Activity Time							
		0700– 0830	0830– 1000	1000– 1130	1130– 1300	1300– 1430	1430– 1600	1600– 1730	1730– 1900
Lizards sampled in the forest									
<i>A. allogus</i>	161	0.08	0.09	0.15	0.21	0.15	0.12	0.12	0.08
<i>A. alutaceus</i>	44	0.02		0.16	0.09	0.27	0.21	0.07	0.18
<i>A. angusticeps</i>	10			0.35	0.45	0.20			
<i>A. barbatus</i>	5			0.20		0.20	0.60		
<i>A. homolechis</i>	119	0.03	0.08	0.17	0.13	0.15	0.18	0.16	0.10
<i>A. loysianus</i>	20				0.15	0.45	0.20	0.15	0.05
<i>A. luteogularis</i>	31			0.18	0.23	0.21	0.19	0.16	0.03
<i>A. mestrei</i>	119	0.03	0.08	0.13	0.24	0.18	0.13	0.11	0.11
<i>A. porcatus</i>	15			0.20	0.07	0.03	0.50	0.13	0.07
<i>A. sagrei</i>	55			0.07	0.39	0.04	0.26	0.19	0.05
<i>A. vermiculatus</i>	8			0.50			0.44	0.06	
Lizards sampled outside of the forest									
<i>A. homolechis</i>	210		0.07	0.17	0.40	0.13	0.21	0.03	0.01
<i>A. porcatus</i>	21		0.05	0.57	0.10	0.10	0.10	0.10	
<i>A. sagrei</i>	114	0.04	0.11	0.20	0.23	0.09	0.17	0.17	0.00

TABLE 8. AVERAGE MOVES PER MINUTE, FREQUENCIES OF THREE LOCOMOTOR BEHAVIORS, AND FREQUENCY OF DISPLAY BEHAVIOR IN 11 *ANOLIS* SPECIES AT SOROA. SAMPLE SIZE IS THE NUMBER OF INDIVIDUAL LIZARDS OBSERVED. ANIMALS THAT MOVED < 5 TIMES WERE NOT INCLUDED IN THE ANALYSIS OF THE FREQUENCIES OF THE LOCOMOTOR BEHAVIORS. IN ADDITION, ONLY INDIVIDUALS OBSERVED BY JBL WERE INCLUDED IN CALCULATIONS OF PERCENTAGES OF MOVES THAT WERE RUNS VERSUS WALKS TO PROVIDE CONSISTENCY WITH PREVIOUS RESEARCH. AS A RESULT, THE FREQUENCIES OF RUNS, WALKS, AND JUMPS DO NOT SUM TO 1.0. DATA WERE COLLECTED ONLY FROM ADULT MALES, EXCEPT FOR *A. BARBATUS*, FOR WHICH DATA (FROM LEAL AND LOSOS, 2000) WERE COLLECTED FROM SUBADULT AND ADULT MALES AND FEMALES; PERCENT TIME DISPLAYING FOR THIS SPECIES IS BASED ON TWO SMALL MALES. DATA ON MOVEMENTS PER MINUTE FOR ALL SPECIES EXCEPT *A. VERMICULATUS* WERE PREVIOUSLY PUBLISHED IN JOHNSON *ET AL.* (2008).

<i>Anolis</i> Species	N	Moves/Min	Jump	Run	Walk	Display
<i>A. allogus</i>	15	0.51	0.14	0.46	0.07	0.037
<i>A. alutaceus</i>	8	0.64	0.56	0.13	0.35	0.008
<i>A. angusticeps</i>	2	2.49	0.09	0.09	0.82	0.020
<i>A. barbatus</i>	7	—	~ 0.001	~ 0.10	0.89	0.078
<i>A. homolechis</i>	21	0.67	0.24	0.44	0.45	0.075
<i>A. loysianus</i>	6	1.83	0.06	0.41	0.52	0.065
<i>A. luteogularis</i>	6	0.62	0.14	0.15	0.72	0.021
<i>A. mestrei</i>	15	0.59	0.28	0.27	0.45	0.068
<i>A. porcatus</i>	11	1.52	0.23	0.21	0.59	0.037
<i>A. sagrei</i>	19	0.57	0.19	0.27	0.49	0.125
<i>A. vermiculatus</i>	7	0.88	0.23	0.22	0.55	0.023

Anolis allogus

Photo by Kevin de Queiroz.

This species fits the classic definition of a trunk-ground anole: a stocky lizard with long hindlimbs, often found perching on broad surfaces (usually tree trunks) relatively close to the ground. *Anolis allogus* is found primarily in deep forest and has a lower body temperature than some of the other trunk-ground anoles. It is one of four sympatric trunk-ground species at Soroa (the others being *A. homolechis*, *A. mestrei*, and *A. sagrei*), which differ in the color of the dewlap and, to a lesser extent, of the body. The dewlap pattern of *A. allogus* exhibits a significant amount of geographic variation across Cuba. At Soroa, the dewlap is primarily yellow, with three to four well-delimited transverse brick-colored bars. The bars are usually located on the upper to middle region of the dewlap.

Anolis alutaceus

Photos courtesy of Luke Mahler.

This species is a small anole usually found on narrow diameter substrates, such as bushes, ferns, or vines, from near the ground to several meters high. The species moves by slow walks and fast jumps. Like most grass-bush anoles, it sports an extraordinarily long tail, as much as 2.5 times

the SVL, as well as long hind limbs. Its irises are blue, and its dewlap is a solid yellow.

Anolis angusticeps

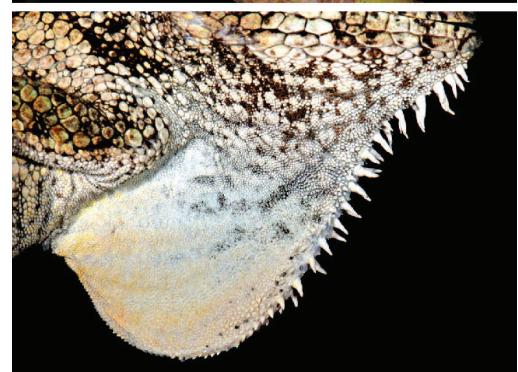


Lizard photograph by Kevin de Queiroz; dewlap photograph courtesy of Luke Mahler.

Small and with short legs, this species fits the classic morphological description of a twig anole. *Anolis angusticeps* has been studied intensively in the Bahamas, where it primarily uses narrow-diameter vegetation

(Schoener, 1968; Irschick and Losos, 1996). However, despite our extensive searching of narrow surfaces, in 30.4% of our observations it perched on trunks and in relatively few observations was it found on narrow surfaces. Whether these observations represent a true difference between Cuban and Bahamian populations of this species, or whether we simply failed to observe these lizards on narrow surfaces—perhaps out of sight high in the canopy—remains to be determined. Like other twig anoles, the *A. angusticeps* we observed moved slowly, rarely running or jumping (except when fleeing perceived predators). The dewlap of this species is peach in color.

Anolis barbatus



Photos courtesy of Luis Díaz.

A member of the *Chamaeleolis* subclade of anoles, *A. barbatus* is large and heavy-bodied. It is a slow-moving animal that often adopts a rocking motion, much like

that seen in chameleons. It is usually found high in trees, but descends to the ground to feed on hard-bodied prey such as mollusks and beetle pupae. This species is often found on surfaces that are relatively narrow for its large size; for this and other reasons, such as the rarity of jumping or running, it may be considered a large twig anole (Leal and Losos, 2000; Losos, 2009). Observations on this species at Soroa were reported in Leal and Losos (2000). The dewlap of *A. barbatus* is white with a pink- to peach-colored edge. Males and females have dewlaps of equivalent size, an unusual characteristic in *Anolis* that is shared with *A. luteogularis*.

Anolis homolechis



Photo by Kevin de Queiroz.

This trunk-ground anole is found in light shade in the forest and in patches of woodland and vegetated perches in open areas. It has a lower body temperature than *A. sagrei*, but a higher body temperature than the deep-forest trunk-ground anoles *A. allogus* and *A. mestrei*. In all respects, it is a typical trunk-ground anole, usually perching close to the ground on tree trunks or other broad structures. *Anolis homolechis* has a solid white dewlap that is brighter than that of *A. barbatus*. On close examination, the dewlap of *A. homolechis* has numerous small black dots between the scales, most likely pockets of melanin. In

some populations, the dewlap appears gray, possibly because of a higher melanin concentration.

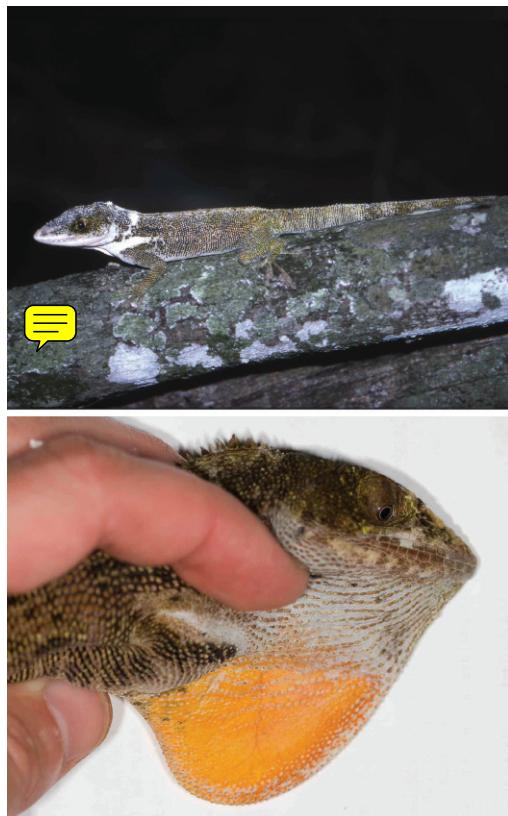
Anolis loysianus



Lizard photograph by Jonathan Losos; dewlap photo courtesy of Luis Díaz.

This small-bodied species is found only on very broad trunks with rugose bark. Like the trunk anoles of Hispaniola, the only other Greater Antillean Island on which the trunk ecomorph occurs, it moves frequently, rarely jumps, and sometimes ascends to great heights. Its crypticity, heightened by fleshy projections on its body, might also contribute to its apparent rarity. It has a pale orange-red dewlap; individual variation is considerable in the number of orange spots, which are scattered across the dewlap and might contribute to the dewlap's saturated appearance.

Anolis luteogularis



Lizard photograph by Kevin de Queiroz; dewlap photograph courtesy of Luke Mahler.

This large-bodied lizard is the longest and heaviest anole at Soroa. It will eat anything it can catch and has been observed stalking other anoles. Normally found high in trees on broad substrates such as trunks and large branches, it descends to lower heights to forage. Most likely, individuals maintain a large home range that encompasses many trees. This species generally moves by walking but will jump or run as necessary. *Anolis luteogularis* also shows the most pronounced response to large avian predators, moving to the underside of a branch and remaining immobile for a few minutes when a red-tailed hawk (*Buteo jamaicensis*) flies overhead. The

dewlap is a pale yellow, sometimes so pale that it almost looks white. Males and females have dewlaps of equivalent size.

Anolis mestrei



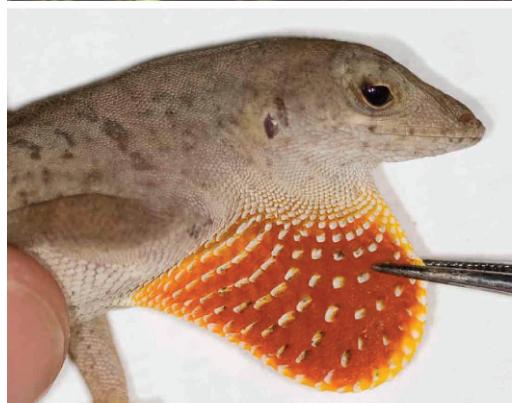
Photo by Kevin de Queiroz.

Morphologically similar to the other trunk-ground members of the *A. sagrei* clade at Soroa, *A. mestrei* is associated with large boulders and limestone walls in the forest. When not found on rocky surfaces, it is usually found on tree trunks. On all surfaces, it is found relatively low to the ground, like other trunk-ground anoles. This species is only found in deep forest and, like *A. allogus*, exhibits relatively low body temperatures. The dewlap pattern of *A. mestrei* exhibits a significant amount of geographic variation across Cuba. At Soroa, the dewlap is two-toned, with a bright white edge and a relatively large brick-red center. Individual variation on the size and saturation of the brick-red center is substantial.

Anolis porcatus

Lizard photograph by Kevin de Queiroz; dewlap photograph of a specimen from the vicinity of Mariel, Cuba, courtesy of Luke Mahler.

This trunk-crown anole is commonly found in human-disturbed habitats, where it is seen on walls, palms, and other trees, ≥ 2 m above the ground. This species also moves frequently on leafy vegetation. *Anolis porcatus* is less commonly seen in the forest, where it is often in the canopy. This species usually has a high body temperature and is often seen basking; individuals readily change their body color between green and brown. It has a relatively small, one-toned dewlap with reddish pink coloration.

Anolis sagrei

Lizard photograph by Kevin de Queiroz; dewlap photograph courtesy of Luke Mahler.

The body temperature of this sun-loving species is only rivaled at Soroa by that of the equally sun loving *A. porcatus*. *Anolis sagrei* is extremely common in human-disturbed areas. Like the other trunk-ground anoles, it is found near the ground, but it perches on practically any surface, from broad tree trunks to

relatively narrow chain link fences. It rarely gets far into the forest, though it might occasionally be seen in open areas within the forest. The dewlap pattern of *A. sagrei* exhibits substantial geographic variation across Cuba. At Soroa, the dewlap is a bright reddish-orange, with prominent yellow scales.

Anolis vermiculatus



Lizard photograph by Jonathan Losos; dewlap photograph courtesy of Luke Mahler.

One of the most remarkable of the more than 360 anole species, *A. vermiculatus* is always found near rivers (Leal *et al.*, 2002), into which it dives to escape predators or to pursue prey, including small fish and shrimps. In a survey of stomach contents, Rodríguez

Schettino and Novo Rodríguez (1985) found insects, crustaceans, and plant matter (flowers and fruits of palms, primarily in the stomachs of adult males). The species will run bipedally across the river surface; individuals can be seen crisscrossing as they chase each other in territorial disputes. When not in the water, these lizards perch on vertical rock walls and on tree branches, from which they dive into the water if threatened, as well as on rock outcrops within the stream (Rodríguez Schettino *et al.*, 1987). This is one of two anoles completely lacking a dewlap (the other is its sister species, *A. bartschi*). Individuals use shallow head bobs to signal to each other; their complex body coloration might aid in communication (Fitch and Henderson 1987). The skin of this species has a velvety texture that might have some relationship to its aquatic habitats.



DISCUSSION

Natural selection often favors ecological divergence that minimizes the intensity of negative interspecific interactions among sympatric species in a community (Hutchison, 1959; MacArthur, 1972; Losos *et al.*, 2003). The lizards of Soroa likely have a long history of ecological interactions (Losos *et al.*, 2003). Our previous work, based on data reported and elaborated on here, revealed

that species are more dissimilar than expected by chance; in particular, species that are similar along one niche axis tend to be dissimilar along another (Losos *et al.*, 2003). The evolution of ecological differences among the anoles living in the same community was predicted by Rand and Williams (1969) on the basis of their study of another complex community of *Anolis* lizards. Williams (1972) coined the term “ecomorph” for groups of species with similar morphology and ecology; he also proposed six ecomorphs for *Anolis* lizards from the Greater Antilles.

The *Anolis* community of Soroa is composed of species representing Williams’ six ecomorph classes (see Losos [2009] for a review of the ecomorph concept): crown-giant, *A. luteogularis*; trunk-crown, *A. portoricensis*; trunk, *A. loysianus*; trunk-ground, *A. allogus*, *A. homolechis*, *A. mestrei*, and *A. sagrei*; twig, *A. angusticeps* (but see qualifications above); and grass-bush, *A. alutaceus*. *Anolis barbatus*, although much larger than other species classified as twig anoles, is similar to twig anoles in many morphological and behavioral respects; moreover, it often uses surfaces that are narrow relative to its size. For this reason, *A. barbatus* might be considered a twig anole (Losos, 2009). *Anolis vermiculatus* does not fit neatly into any of the six standard Greater Antillean ecomorph categories, although it selects perch sites similar to those used by trunk-ground anoles. However, other anoles, both in the Greater Antilles (*A. eugenegrahami* from Hispaniola) and on the mainland (a number of species) are similar to *A. vermiculatus* in being found only near streams. The two Greater Antillean species, however, are not similar morphologically, and neither is similar to those on the mainland. For this reason, these “semiaquatic” anoles do not constitute an ecomorph class *sensu* Williams (Leal *et al.*, 2002).

Our results indicate that, regardless of whether competition is an important factor in the structuring of the anole communities, differences in the use of resources among the species from Soroa are sufficient to allow 11 species to coexist in what seems to be a stable community.

Comparisons to Previous Work on These Species

Although the body temperatures of several *Anolis* species occurring at Soroa have been reported previously (Rodríguez Schettino, 1999a), only the data for *A. mestrei* (Rodríguez Schettino and Chamizo Lara, 2001) and those for *A. vermiculatus* (González Bermúdez and Rodríguez Schettino, 1982; Rodríguez Schettino *et al.*, 1987; Rodríguez Schettino and Martínez Reyes, 1989) had actually been collected at Soroa, as opposed to elsewhere in Cuba. Data for *A. homolechis* and *A. allogus* (Silva Rodríguez, 1981) were collected at nearby locations in the Sierra del Rosario. *Anolis mestrei* body temperatures at Soroa in June 1995 (Rodríguez Schettino and Chamizo Lara, 2001) were similar to those that we recorded (means of 28.2°C vs. 27.5°C, respectively). Body temperatures for *A. homolechis* elsewhere in the Sierra del Rosario generally were higher than those reported here (means of 32.1°C vs. 29.2°C, respectively), but the values were similar for *A. allogus* (means of 27.5°C vs. 26.9°C, respectively). *Anolis vermiculatus* body temperatures were taken by González Bermúdez and Rodríguez Schettino (1982) during the dry season, and it is not possible to compare their data with ours; however, Rodríguez Schettino *et al.* (1987) and Rodríguez Schettino and Martínez Reyes (1989) obtained their data for June 1983 (mean 26.0°C) and June 1986 (mean 28.6°C), respectively. Both values are lower than the mean we report (29.4°C), probably reflecting differences in the weather among the 3 years in which data were gathered.

Ruibal (1961) reported body temperatures for three of the species at various sites in eastern Cuba. He collected data in July and August, recording mean body temperatures of 29.2°C for *A. allogus*, 31.8°C for *A. homolechis*, and 33.1°C for *A. sagrei*. These values are all somewhat higher than the means for these species reported here; we assume that the differences reflect seasonal or geographical variation.

With regard to the vegetation types that the 11 anole species occupy, our results partially mirror those of Martínez Reyes (1995), although we found several species in a wider range of habitats than she did. In both studies, *A. homolechis* was found in the planted woodland, as well as in all three forest vegetation types; *A. mestrei* and *A. vermiculatus* only in the gallery forest; *A. loysianus* only in the evergreen forest; and *A. alutaceus* only in secondary vegetation. However, Martinez found *A. allogus* only in the evergreen forest, whereas we discovered it in all three vegetation types. Similarly, although Martinez found *A. sagrei* only around human constructions, we also found it in the gallery forest. In addition, Martínez Reyes (1995) found *A. porcatus*, *A. hiteogularis*, and *A. angusticeps* only in secondary vegetation, whereas we found the former species also in the gallery forest and the latter two species in all three vegetation types. She did not detect *A. barbatus* in the gallery forest, whereas we did. Although Martinez did not find the grass-bush anole *Anolis ophiolepis* (Fig. 1) at Soroa, Rodríguez Schettino *et al.* (2005) found two individuals in secondary vegetation, and we found one individual in grassy secondary vegetation along a roadside near Soroa while collecting at night.

With regard to substrates used, our results more closely resemble those of Martínez Reyes (1995), but we found a wider range of microhabitat use in some species. She did not find *A. homolechis*, *A. sagrei*, or *A. vermiculatus* on rocks, nor did she encounter



Figure 1. *Anolis ophiolepis*. Photograph by Kevin de Queiroz of a specimen collected in Havana, Cuba.

A. homolechis, *A. mestrei*, or *A. allogus* on or around human constructions. In addition, she found *A. alutaceus* on grasses, whereas we only observed this species in the forest, where it primarily perched on narrow branches, lianas, and ferns. Martínez Reyes did not report data on perch height or body temperature. Our results on perch height generally coincide with the findings of Rodríguez Schettino (1999a, b) and Rodríguez Schettino and de Queiroz (2002a, b). All of the species at Soroa were observed in the sun or shade at frequencies similar to those reported by Rodríguez Schettino (1999a).

CONCLUSIONS

Research on anoles has played an important role in the development of community ecological theory (e.g., Schoener, 1968, 1974, 1977). Until now, no comprehensive study had been conducted on Cuban anole communities, even though Cuba hosts the richest and most diverse anole fauna in the West Indies. Our data indicate that at least one Cuban anole community follows the same patterns documented in less species-rich communities on other islands in the West Indies. Nonetheless, further work is needed

on localities elsewhere in Cuba; indeed, little is known about how anole communities differ among localities within a single island. In addition, the anole fauna of mainland Central and South America is as diverse as that on the islands, yet many differences exist between mainland and island anoles (Andrews, 1979; Pinto *et al.*, 2008; reviewed in Losos, 2009). Detailed studies of mainland anole communities could prove very informative with regard to understanding how these differences have arisen.

ACKNOWLEDGMENTS

We thank Adela Torres Barboza and Ángel Daniel Álvarez for their assistance with field work and Luis Díaz and Luke Mahler for allowing us to use their photographs. We received funds for this work from the “Programa Nacional de Ciencia y Técnica de Los Cambios Globales y la Evolución del Medio Ambiente Cubano,” the National Geographic Society (grants 5639-96 and 6981-01), the National Science Foundation, and a faculty grant from Barnard College.

LITERATURE CITED

- ANDREWS, R. M. 1979. Evolution of life histories: A comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora* **454**: 1–51.
- CAPOTE, R. P. 1989. La vegetación de la Sierra del Rosario. Ph.D. Dissertation, La Habana, Cuba, Instituto de Ecología y Sistemática.
- DÍAZ, L. M., N. NAVARRO, AND O. H. GARRIDO. 1998. Nueva especie de *Chamaeleolis* (Sauria: Iguanidae) de la Meseta de Cabo Cruz, Granma, Cuba. *Avicennia* **8/9**: 27–34.
- FITCH, H. S., AND R. W. HENDERSON. 1987. Ecological and ethological parameters in *Anolis bahorucoensis*, a species having rudimentary development of the dewlap. *Amphibia-Reptilia* **8**: 69–80.
- GARRIDO, O. H., AND S. B. HEDGES. 2001. A new anole from the northern slope of the Sierra Maestra in eastern Cuba (Squamata: Iguanidae). *Journal of Herpetology* **35**: 378–383.
- GONZÁLEZ BERMÚDEZ, F. M., AND L. RODRÍGUEZ SCHETTINO. 1982. Datos etoecológicos sobre *Anolis vermiculatus* (Sauria: Iguanidae). *Poeyana* **245**: 1–18.
- HASS, C. A., S. B. HEDGES, AND L. R. MAXSON. 1993. Molecular insights into the relationships and biogeography of West Indian anoline lizards. *Biochemical Systematics and Ecology* **21**: 97–114.
- HEATWOLE, H. 1982. A review of structuring in herpetofaunal assemblages. U. S. Fish and Wildlife Service Wildlife Research Report **13**: 1–19.
- HERTZ, P. E. 1991. Evaluating thermal resource partitioning by sympatric lizards *Anolis cooki* and *A. cristatellus*: A field test using null hypotheses. *Oecologia* **90**: 127–136.
- HUEY, R. B., C. DEUTSCH, J. J. TEWKSURY, L. J. VITT, P. E. HERTZ, H. J. ALVAREZ PEREZ, AND T. GARLAND, JR. 2009. Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society B* **276**: 1939–1948.
- HUTCHISON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**: 145–159.
- IRSCHICK, D. J., AND J. B. LOSOS. 1996. Morphology, ecology, and behavior of the twig anole, *Anolis angusticeps*, pp. 291–301. In R. Powell and R. W. Henderson (eds.), *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz*. Ithaca, New York, Society for the Study of Amphibians and Reptiles.
- JACKMAN, T., A. LARSON, K. DE QUEIROZ, AND J. B. LOSOS. 1999. Phylogenetic relationships and tempo of early diversification in *Anolis* lizards. *Systematic Biology* **48**: 254–285.
- JENSSSEN, T. A., D. L. MARCELLINI, AND E. P. SMITH. 1988. Seasonal micro-distribution of sympatric *Anolis* lizards in Haiti. *Journal of Herpetology* **22**: 266–274.
- JOHNSON, M. A., M. LEAL, L. RODRÍGUEZ SCHETTINO, A. CHAMIZO LARA, L. J. REVELL, AND J. B. LOSOS. 2008. A phylogenetic perspective on foraging mode evolution and habitat use in West Indian *Anolis* lizards. *Animal Behaviour* **75**: 555–563.
- LEAL, M., AND L. FLEISHMAN. 2002. Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proceedings of the Royal Society of London B* **269**: 351–359.
- , AND J. B. LOSOS. 2000. Behavior and ecology of the Cuban “chipojos bobos” *Chamaeleolis barbatus* and *C. porcus*. *Journal of Herpetology* **34**: 318–322.
- , A. K. KNOX, AND J. B. LOSOS. 2002. Lack of convergence in aquatic *Anolis* lizards. *Evolution* **56**: 785–791.

- Losos, J. B. 1990. Concordant evolution of locomotor behaviour, display rate, and morphology in *Anolis* lizards. *Animal Behaviour* **39**: 879–890.
- . 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Systematic Biology* **41**: 403–420.
- . 2009. Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles. Berkeley, California, University of California Press.
- , AND L.-R. CHU. 1998. Examination of factors potentially affecting dewlap size in Caribbean anoles. *Copeia* **1998**: 430–438.
- , M. LEAL, R. E. GLOR, K. DE QUEIROZ, P. E. HERTZ, L. RODRÍGUEZ SCHETTINO, A. CHAMIZO LARA, T. R. JACKMAN, AND A. LARSON. 2003. Niche lability in the evolution of a Caribbean lizard community. *Nature* **424**: 542–545.
- MACARTHUR, R. 1972. Geographical Ecology: Patterns in the Distribution of Species. Princeton, New Jersey, Princeton University Press.
- MARTÍNEZ REYES, M. 1995. Saurios de la Reserva de la Biosfera “Sierra del Rosario” Pinar del Río, Cuba. Evaluación ecológica de tres comunidades. *Investigaciones Geográficas Boletín* **30**: 50–77.
- NICHOLSON, K. E., L. J. HARMON, AND J. B. LOSOS. 2007. Evolution of *Anolis* lizard dewlap diversity. *PLoS One* **2**(3): e274.
- PINTO, G., D. L. MAHLER, L. J. HARMON, AND J. B. LOSOS. 2008. Testing the island effect in adaptive radiation: rates and patterns of morphological diversification in Caribbean and mainland *Anolis* lizards. *Proceedings of the Royal Society B* **275**: 2749–2757.
- POWELL, R., J. S. PARMERLEE, JR., AND D. D. SMITH. 1996. Evidence of spatial niche partitioning by a Hispaniolan lizard community in a xeric habitat, pp. 317–326. In R. Powell and R. W. Henderson (eds.), Contributions to West Indian Herpetology: A tribute to Albert Schwartz. Ithaca, New York, Society for the Study of Amphibians and Reptiles.
- RAND, A. S. 1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* **45**: 745–752.
- . 1967. Ecology and social organization in the iguanid lizard *Anolis lineatopus*. *Proceedings of the United States National Museum* **122**: 1–79.
- , AND E. E. WILLIAMS. 1969. The anoles of La Palma: aspects of their ecological relationships. *Breviora* **327**: 1–17.
- , AND —. 1970. An estimation of redundancy and information content of anole dewlaps. *The American Naturalist* **104**: 99–103.
- RODRÍGUEZ SCHETTINO, L. 1999a. Systematic accounts of the species, pp. 104–380. In L. Rodríguez Schettino (ed.), The Iguanid Lizards of Cuba. Gainesville, Florida, University of Florida Press.
- . 1999b. Morfometría, distribución geográfica y microhabitat de los lagartos del género *Anolis* (Lepidoasuridae: Iguania). Ph.D. Dissertation. La Habana, Cuba, Instituto de Ecología y Sistemática.
- , AND A. CHAMIZO LARA. 2001. *Anolis mestrei* (NCN). Thermal habitat. *Herpetological Review* **32**: 253.
- , —, V. RIVALTA GONZÁLEZ, C. MANCINA GONZÁLEZ, AND A. HERNÁNDEZ MARRERO. 2005. Herpetofauna de la Reserva de la Biosfera “Sierra del Rosario”, Cuba. *Poeyana* **493**: 12–16.
- , AND K. DE QUEIROZ. 2002a. *Anolis homolechis homolechis* (NCN). Thermal biology and microhabitat. *Herpetological Review* **33**: 304.
- , AND —. 2002b. *Anolis sagrei sagrei* (Cuban brown lizard; Chino; Torito). Habitat use and thermal biology. *Herpetological Review* **33**: 305.
- , C. A. MANCINA GONZÁLEZ, E. PÉREZ MENA, A. CHAMIZO LARA, A. MARTELL GARCIA, AND A. HERNÁNDEZ MARRERO. 1999. Bases para el futuro manejo y conservación de los vertebrados terrestres de la Reserva de la Biosfera Sierra del Rosario. *Scientific Report*, La Habana, Cuba, Instituto de Ecología y Sistemática.
- , D. L. MARCELLINI, AND J. NOVO RODRÍGUEZ. 1987. Algunos aspectos ecológicos sobre *Anolis vermiculatus* (Sauria: Iguanidae) en Soroa, Pinar del Rio, Cuba. *Poeyana* **343**: 1–9.
- , AND M. MARTÍNEZ REYES. 1989. Algunos aspectos ecológicos sobre cuatro especies endémicas del género *Anolis* (Sauria: Iguanidae). *Scientific Report*, La Habana, Cuba, Instituto de Ecología y Sistemática.
- , AND J. NOVO RODRÍGUEZ. 1985. Nuevos dato etoecológicos sobre *Anolis vermiculatus* (Sauria: Iguanidae). *Poeyana* **296**: 1–11.
- , AND V. RIVALTA GONZÁLEZ. 2007. Efectos probables del aumento del nivel del mar sobre la herpetofauna de la Reserva de la Biosfera Ciénaga de Zapata, Matanzas, Cuba. *Poeyana* **495**: 8–13.
- ROUGHGARDEN, J., W. PORTER, AND D. HECKEL. 1981. Resource partitioning of space and its relationship to body temperatures in *Anolis* lizard populations. *Oecologia* **50**: 256–264.
- RUIBAL, R. 1961. Thermal relations of five species of tropical lizards. *Evolution* **15**: 98–111.
- SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**: 474–477.

- . 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**: 704–726.
- . 1974. Resource partitioning in ecological communities. *Science* **185**: 27–39.
- . 1977. Competition and the niche, pp. 35–136. In C. Gans and D. W. Tinkle (eds.), *Biology of the Reptilia*, volume 7, New York, Academic Press.
- . AND G. C. GORMAN. 1968. Some niche differences among three species of Lesser Antillean anoles. *Ecology* **49**: 819–830.
- SILVA RODRÍGUEZ, A. 1981. Estudio del nicho estructural, climático y temporal de dos especies del género *Anolis* (Sauria: Iguanidae), p. 185. In Abstracts of the First National Congress of Biology, La Habana, Cuba.
- WILLIAMS, E. E. 1972. The origin of faunas: evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology* **6**: 47–89.
- . 1976. West Indian anoles: a taxonomic and evolutionary summary. 1. Introduction and a species list. *Breviora* **440**: 1–21.
- . 1983. Ecomorphs, faunas, island size, and diverse end points in island radiation of *Anolis*, pp. 326–370. In R. B. Huey, E. R. Pianka and T. W. Schoener (eds.), *Lizard Ecology: Study of a Model Organism*. Cambridge, Massachusetts, Harvard University Press.