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## Seasonal Micro-distribution of Sympatric *Anolis* Lizards in Haiti

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**ABSTRACT.**—A new cluster census method was used to examine the intra- and interspecific micro-distributions of two syntopic lizards, *Anolis cybotes* and *Anolis caudalis*, across seasons (November, June). Numbers of *A. caudalis* were very stable across seasons; males slightly outnumbered females (1.2 sex ratio). In contrast *A. cybotes* had a 1:1 sex ratio in November, then numbers of male *A. cybotes* dramatically declined by June, resulting in a 2:3 ratio. We speculate that this was related to pronounced territorial behavior. Female *A. cybotes* were more closely associated with males in June (breeding season) than in November, resulting in multiple females per male in the breeding season.

There was some partitioning of the structural habitat by species and sex classes which, for the most part, was stable between seasons. In general, the smaller *A. caudalis* preferred high perches (>2 m) on large trees, while *A. cybotes* perched under 2 m. Male *A. cybotes* also had a preference for large trees. Female *A. cybotes*, on the other hand, used all available vegetative structures without preference, and tended to perch below conspecific males ( $\bar{x}$  = 1 m). Quantification of habitat partitioning, however, indicated much overlap among species-sex classes. Most habitat overlap coefficients were high (.90-.99). Discriminant analysis produced few significant differences between lizard classes, with poor discrimination of niche uniqueness. *Anolis cybotes* males had the least discrete habitat niche (10% discrimination).

The expectation of male *A. cybotes* (large and aggressive) dominating the smaller *A. caudalis* did not materialize. Data did not indicate any obvious interspecific competition as niche overlap values did not vary much with season and population density. In June when male *A. cybotes* are territorial, the habitat niches of other classes of lizards did not change significantly from November values, or they shifted toward that of *A. cybotes*.

Interspecific interaction is a central issue for explaining the spatial relationships of sympatric assemblages of similar species (reviews of Schoener, 1983; Strong et al., 1984). *Anolis* lizards, in particular, have been used to demonstrate the effects of competitive interactions on niche partitioning (reviews of Heatwole, 1977; Schoener, 1977, 1982). The detection of intra- and interspecific interactions has rested prominently upon the extent of niche overlap or niche shifts of suspected competitors (e.g., Talbot, 1979; Jenssen et al., 1984; Salzburg, 1984; Pacala and Roughgarden, 1985; review of Schoener, 1975), with perch site measurements (i.e., structural habitat) being commonly used niche dimensions.

We elected to examine the structural habitat of two common *Anolis* lizards in Haiti, *A. cybotes* and *A. caudalis*, which are sexually dimorphic in size and whose microhabitats overlap broadly along the "ground-trunk" structural niche (sensu Rand and Williams, 1969; Williams, 1972). Of these two co-existing species, *A. cybotes*

males are the largest of the species-sex classes and *A. caudalis* females are the smallest. We hypothesized that the male *A. cybotes*, known to be quite aggressive (Jenssen, 1983; Losos, 1985), would be the dominant size class of lizard in its structural niche. Also, if territoriality is a component of intra- and interspecific interactions, then a different spatial configuration and increased agnostic behavior should appear during the breeding (wet) season as compared with the non-breeding (dry) season (Ruibal et al., 1972; Gorman and Licht, 1974; Stamps and Crews, 1976; Stamps, 1977; Rose, 1982).

To investigate the *cybotes-caudalis* assemblage for perch shifts and general influence of male *A. cybotes* on adjacent anoles, we recorded the spatial relationships of *A. cybotes* males: (1) among themselves; (2) with female conspecifics; and (3) with male and female *A. caudalis*. These micro-distributions were then compared across seasons to investigate effects of the breeding and non-breeding periods on perch char-

acteristics, as well as the stability of population sizes within species and sex classes. A new cluster census method was devised to quantify the above comparisons.

#### MATERIAL AND METHODS

*Anolis cybotes* and *A. caudalis* are sexually dimorphic in size and are of the following average adult snout-vent lengths: 15 *A. cybotes* males, 62 mm (range 54–69 mm); 15 *A. cybotes* females, 47 mm (range 41–52 mm); 15 *A. caudalis* males, 48 mm (range 45–51 mm); and 15 *A. caudalis* females, 40 mm, (range 37–45 mm). The species were studied on the property of the Kalico Beach Club on Route 100, 55 km north of Port-au-Prince, Haiti. This private property provided isolation from human interference and a measure of protection for the habitat and fauna, facilitating a longitudinal study. The study area was composed of discontinuous habitat due to the xeric climate and the semi-cultivated state of the grounds. Many of the trees, shrubs, and vines were separated by low ground cover.

Data were collected from the same study area (approx. 1.2 ha) during the dry season (11–25 November 1983) and the wet season (15–29 June 1984). During each of the two seasons, 30 non-overlapping clusters of observations (mini-censuses) were made while criss-crossing the study area. Each of these mini-censuses was conducted in the following manner. The location of an adult male *A. cybotes* served as a "focal animal" and the center of a mini-census. We recorded the size rank of the vegetation he was on (Fig. 1A) and his species, sex, relative size (adult, subadult, or juvenile), perch height (to nearest 0.1 m), and perch diameter (to nearest cm). The same data were recorded for all other *A. cybotes* and *A. caudalis* found on the same clump of vegetation with the focal animal. We then recorded: (1) the distance from the focal animal's perch to each of the next four closest clumps of vegetation (i.e., "sampling stations" as shown in Fig. 2); (2) the vegetation rank of each of these sampling stations; and (3) the species, sex, size, perch height, and perch diameter of any *A. cybotes* and *A. caudalis* that were residing on each of these sampling stations. Taken to-

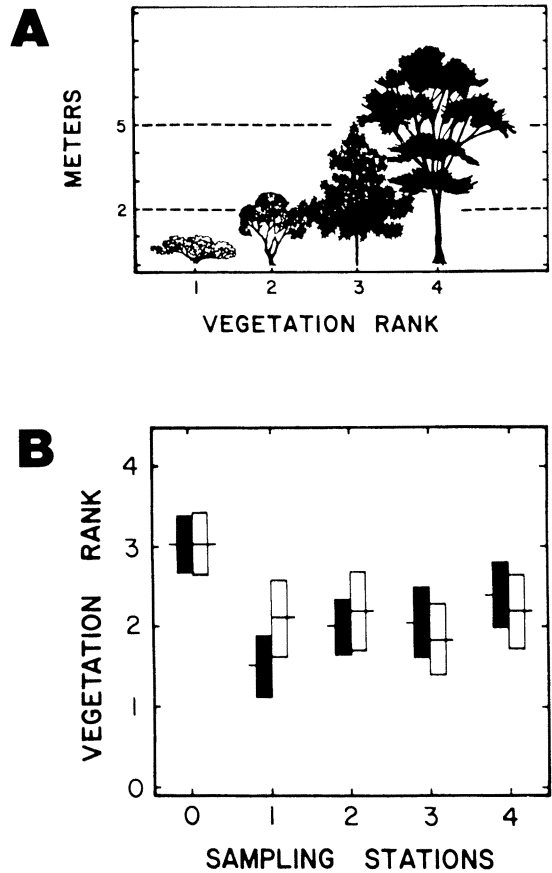


FIG. 1. A. Ranking microhabitat according to size and complexity, where small shrubs (<2 m) = 1, large shrubs (>2 m) = 2, small trees (<5 m) = 3, and large trees (>5 m) = 4. B. Mean (horizontal line) and 95% confidence limits (ends of bars) for the size rank of vegetation found within the focal (0) and next four sampling stations (1–4) of 30 census clusters in June (black) and 30 in November (white).

gether, these data constituted one census cluster. Thus, for a given season, 30 clusters were censused, containing a total of 150 sampling stations.

Quantitative analyses of the data were performed on an IBM 3084 computer, using the Statistical Analysis System and Biomedical Computer Programs software packages (Dixon, 1975; Barr et al., 1979). Computation of niche overlap used the following formula (Maurer, 1982):

$$\alpha = \exp[-(\mu_1 - \mu_2)^2 / 4\sigma^2],$$

where  $\alpha = 0$  represents no overlap and  $\alpha = 1$  is complete overlap.



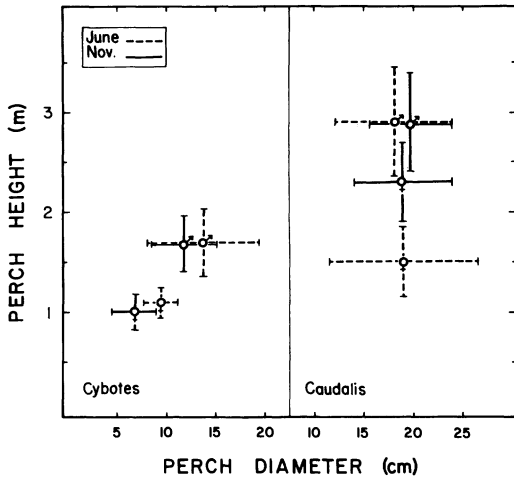


FIG. 3. Male and female means (depicted by ♂ and ♀) and their 95% confidence limits (ends of lines) for adult perch height and perch diameter of: 39 male and 63 female *Anolis cybotes* in June, 85 male and 80 female *A. cybotes* in November, 48 male and 41 female *Anolis caudalis* in June, and 47 male and 39 female *A. caudalis* in November.

abundance. Whereas the adult sex ratio in November was approximately 1 (17:16, male : female), it significantly ( $\chi^2 = 4.71$ ,  $P < 0.05$ ) shifted to a 2:3 ratio in June, with females outnumbering males. Second, the males were also distributed within the clusters differently in June than in November (Fig. 4). We found as many males close to the focal animals (0.2 m away) in November clusters as on the fringe (3–8 m). In June, however, males which shared a cluster with the focal male tended to be in

the periphery of the cluster (5–6 m away). In addition, June males were seen disputing daily (i.e., facing off, vocalizing, jaw locking), whereas these aggressive behaviors were never seen in November.

Adult female *A. cybotes* differed significantly from their conspecific males by perching, on the average, 0.6 m lower than males, and occupying smaller vegetative structures (70% in shrubs), regardless of season (Tables 1 and 2, Fig. 3). This is reflected in the lower niche overlap coefficients when comparing vegetation rank of males with females within seasons (Table 3). Females also demonstrated stable habitat utilization across seasons; all of their overlap values comparing June and November data for perch diameter, perch height, and vegetation rank were .99. The only notable shift with season was the distance females were found from focal males; June females perched closer to these males than did November females (Table 2: 2.1 vs. 3.0 m,  $P < 0.05$ ). Considering there were fewer males in June, this probably resulted in a polygynous mating structure.

Some stratification in habitat usage was found between *A. cybotes* and *A. caudalis*. The majority (74%) of male and female *A. caudalis* were on trees ( $\bar{x}$  vegetation rank = 3.0–3.7, Tables 1 and 2), either on the trunks or limbs. Average perch heights and diameters for *A. caudalis* were more than 2.3 m and 18 cm, respectively (Fig. 3). This resulted in the *A. caudalis* mean perch

TABLE 2. Means and standard error of the means for structural habitat and distributional characteristics of 30 census clusters (see text) for *Anolis cybotes* and *Anolis caudalis* in Haiti.

	<i>A. cybotes</i>			<i>A. caudalis</i>		
	Adult males	Adult females	Juveniles	Adult males	Adult females	Juveniles
June (wet)						
Sample size	39	63	33	48	40	4
Perch height (m)	1.7 ± 0.17	1.2 ± 0.15	0.5 ± 0.11	2.9 ± 0.27	1.5 ± 0.18	0.2 ± 0.06
Perch dia. (cm)	13.7 ± 2.82	8.3 ± 1.81	2.9 ± 0.48	18.2 ± 3.01	19.4 ± 3.89	1.8 ± 1.09
Vegetation rank	3.1 ± 0.15	2.4 ± 0.12	1.5 ± 0.13	3.3 ± 0.14	3.0 ± 0.16	1.8 ± 0.63
Dist-to-center (m)	0.9 ± 0.35	2.1 ± 0.25	2.9 ± 0.36	1.8 ± 0.34	2.4 ± 0.48	3.5 ± 1.67
November (dry)						
Sample size	85	80	5	47	39	0
Perch height (m)	1.7 ± 0.13	1.0 ± 0.09	0.5 ± 0.30	2.9 ± 0.25	2.3 ± 0.22	
Perch dia. (cm)	11.9 ± 1.64	6.7 ± 1.02	3.1 ± 1.44	19.8 ± 2.59	18.8 ± 2.60	
Vegetation rank	2.9 ± 0.13	2.1 ± 0.13	1.3 ± 0.33	3.7 ± 0.10	3.6 ± 0.14	
Dist-to-center (m)	2.3 ± 0.30	3.0 ± 0.27	3.1 ± 0.71	2.1 ± 0.38	2.3 ± 0.44	

TABLE 3. Habitat overlap values for species-sex classes of *Anolis cybotes* and *Anolis caudalis* in the wet (June) and dry (November) seasons.

	June			November		
	Cybotes ♂	Cybotes ♀	Caudalis ♂	Cybotes ♂	Cybotes ♀	Caudalis ♂
Perch diameter						
Cybotes ♂	—			—		
Cybotes ♀	0.991	—		0.958	—	
Caudalis ♂	0.987	0.923	—	0.942	0.778	—
Caudalis ♀	0.983	0.919	0.999	0.954	0.787	0.999
Perch height						
Cybotes ♂	—			—		
Cybotes ♀	0.935	—		0.873	—	
Caudalis ♂	0.862	0.705	—	0.823	0.528	—
Caudalis ♀	0.985	0.981	0.806	0.945	0.653	0.959
Vegetation rank						
Cybotes ♂	—			—		
Cybotes ♀	0.872	—		0.874	—	
Caudalis ♂	0.993	0.812	—	0.856	0.509	—
Caudalis ♀	0.997	0.910	0.982	0.900	0.592	0.996

height being significantly greater than that of *A. cybotes*. However, it was not unusual to find *A. caudalis* perching below *A. cybotes*. In fact, niche coefficients show a rather large overlap of all habitat variables between *A. caudalis* and male *A. cybotes*, with the greater overlap of the two species in June (Table 3). The large overlap in June was primarily due to *A. caudalis* females taking lower perch heights than they held in November (Tables 2 and 3, Fig. 3).

Population stability was much greater for *A. caudalis* than for *A. cybotes*. Numbers of *A. caudalis* males and females were very similar between seasons: 47 and 48 males in November and June, respectively; 39 and 40 females in November and June, respectively. The sex ratio was not significantly different from unity in either season ( $1.2$ ,  $\chi^2 = 1.64$ , n.s.).

Numbers of *A. cybotes* varied considerably across seasons. June was a period of recruitment, with 33 juveniles recorded versus only 5 in November. The juveniles were found in a significantly different part of the structural habitat from adults, residing low ( $\bar{x} = 0.5$  m) in small ( $\bar{x}$  vegetation rank = 1.5), thin structured ( $\bar{x} = 3.0$  cm) vegetation (Table 2). Likewise, juvenile *A. caudalis* were also sighted low in small shrubs (Table 2). Unlike *A. cybotes*, however, few *A. caudalis* young were seen: none in November and only four in June. These small numbers may not reflect the true status of *A. caudalis* reproduction. It is possible that some juveniles reside in the leafy canopy of trees where it is difficult to census.

As a summary analysis, we took the three habitat niche variables and quantitatively examined them for habitat partitioning and seasonal displacements in adult classes, using stepwise discriminant analysis (Dixon, 1975). Vegetation rank was the most di-

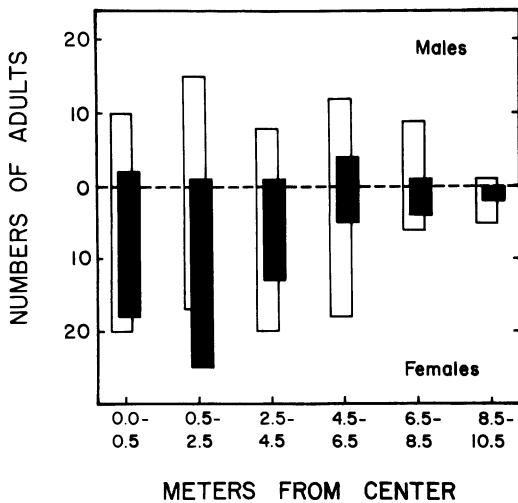


FIG. 4. Distance of adult female and non-focal male *Anolis cybotes* from focal males within 30 census clusters in June (black bars) and 30 in November (white bars).

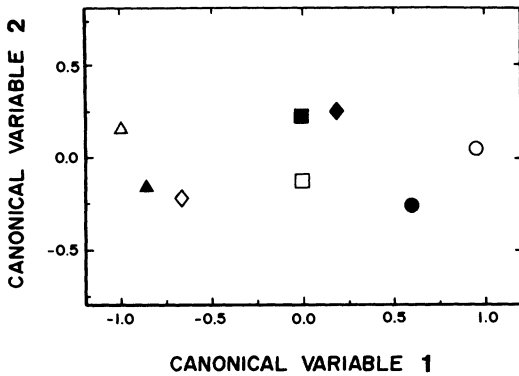


FIG. 5. Discriminant analysis performed with microhabitat variables, vegetation rank, perch height, and perch diameter. Group means shown for male *A. cybotes* (squares), female *A. cybotes* (circles), male *A. caudalis* (triangles), and female *A. caudalis* (diamonds), and their shifts with dry season (white symbols) to wet season (black symbols).

agnostic niche criterion for niche separation in the November censuses and perch height was the best for the June censuses. Nevertheless, the overall analysis showed that there was poor habitat segregation among the lizard classes. The *F*-matrix (Table 4) resulted in very few statistically different niches. Presented graphically (Fig. 5), only June male *A. caudalis* and female *A. cybotes* were significantly different in their habitat niches, and in November the comparisons of male and female *A. caudalis* with female *A. cybotes* were the only ones of significance. Of particular interest were the *A. cybotes* males who broadly overlapped with all lizard classes (Tables 3 and 4, Fig. 5). The classification procedure of the analysis, which provides an empirical measure of the success of habitat discrimination, could correctly assign only 10% of the male *A. cybotes* observations to their proper species-sex class (Table 5). Habitat separation by the other classes was not

TABLE 5. The assignment of 440 individuals to the species-sex niches of male and female *Anolis cybotes* and *Anolis caudalis* by the discriminate analysis classification procedure. Data are given as percentages, with correct classifications underlined.

Species-sex class of individual	Species-sex niche which best matches individual			
	Cybotes ♂	Cybotes ♀	Caudalis ♂	Caudalis ♀
Cybotes ♂	<u>10</u>	40	19	31
Cybotes ♀	5	<u>71</u>	5	19
Caudalis ♂	8	20	<u>47</u>	25
Caudalis ♀	9	30	24	<u>37</u>

much better, ranging from 37–47%. Only female *A. cybotes* observations were most successfully discriminated from the other lizard classes (71%).

When comparing habitat utilization of species-sex classes across seasons (Fig. 5), only female *A. caudalis* showed a significant shift. This shift reflected lower perches on vegetation of smaller rank in June (Tables 1 and 2).

## DISCUSSION

We examined the intra- and interspecific micro-distribution of two sympatric anoline lizards across seasons to: (1) characterize and compare their structural habitat niches and (2) look for effects of season and dominance. Within species, males tended to perch higher than females, a frequently observed characteristic in *Anolis* (Schoener and Schoener, 1971a, b). Such intraspecific partitioning of the habitat, especially in a sexually size dimorphic species as *A. cybotes*, may have evolved to decrease competition for food (review by Schoener, 1987; but see also Trivers, 1976; Floyd and Jensen, 1983; Zucker, 1986).

TABLE 4. *F*-matrix of stepwise discriminant analysis testing for equality among habitat characteristics of male and female *Anolis cybotes* and *Anolis caudalis*.

	June			November		
	Cybotes ♂	Cybotes ♀	Caudalis ♂	Cybotes ♂	Cybotes ♀	Caudalis ♂
Cybotes ♀	6.87			16.50		
Caudalis ♂	8.64	26.46*		18.74	57.47*	
Caudalis ♀	0.39	4.81	12.83	7.12	34.57*	2.95

\* Statistically significant ( $P < 0.05$ ).

The *A. cybotes* males did not use the available habitat in a proportional manner, but showed a preference for large trees. Fifty percent of the males were found on large trees even though this class of vegetation constituted only 26–32% of the censused habitat (Table 1). Presumably, males prefer large perch structures as territorial display areas (Andrews, 1971; Salzburg, 1984); tree trunks are generally free of surrounding vegetation which can disrupt the monitoring of neighbors and transmission of visual signals. In contrast, *A. cybotes* females demonstrated a proportional use of the available microhabitat (Table 1), since they did not seem restricted by a propensity for large vegetative structures as did conspecific males or a requirement for high perch sites as did *A. caudalis*.

Structural niche characteristics of *A. cybotes* were very stable, with minimal differences between seasons. The one variable, however, which changed considerably with season was the number of adult males. There was a six-fold decrease in males sharing a census cluster with the focal male during June (breeding season) as compared with November (non-breeding season). This we attribute primarily to heightened territorial behavior during the June census. We discounted disease or lack of food as likely causes for fewer males because neither conspecific females nor *A. caudalis* within the clusters mirrored this seasonal drop. On the other hand, intermale aggression in *A. cybotes* is known to be intense, with physical attack prevalent, even leading to possible broken jaws (Jenssen, 1983; Losos, 1985). Territorial aggression was seen between males in June and never in November. In June it was rare to find two males within 10 m of each other, while on the average there were two females within 2 m of a male. Therefore, it is likely that June males experienced increase, dispersal and mortality due to territorial behavior. Differential mortality on territorial males could be compounded by predators (e.g., snakes) which are attracted by the frequent displays and movements of resident males (Henderson, 1984; Jim Gillingham, pers. comm.).

Across its geographic distribution, habitat utilization by *A. cybotes* seems to be somewhat flexible. Moermond (1979) reported shifts in microhabitat usage depending upon study site, but he most frequently observed *A. cybotes* on rocks (>80%). This would classify *A. cybotes* as a "ground-trunk" anole. On our study area, there were no rock outcroppings and in 267 sightings we recorded only one *A. cybotes* on the ground. Thus, our observations would characterize the species as a "trunk" anole.

*Anolis caudalis* is definitely a "trunk" anole in that the males were never and the females seldom found in small shrubs, even though this vegetation structure made up 32–40% of the censused microhabitat (Table 1). *Anolis caudalis* tended to be more restricted to large trees than *A. cybotes*, and used higher perch sites. Like *A. cybotes*, there were only minimal seasonal differences in the habitat niche characteristics of *A. caudalis*. Females showed a November to June trend for moving from large trees to large shrubs, with a concomitant decrease in perch height. As a class, this placed them further away from conspecific males during June; one would expect the opposite trend, with an increasing male-female association during the breeding season as observed for female *A. cybotes* (Fig. 4).

Although descriptive statistics (mean values) indicate habitat partitioning among lizards (Fig. 3), there was little discrete separation of class populations. Overlap coefficients for habitat variables were very high (>.9 for most comparisons, Table 3), being in the upper 20th percentile for many lizard communities (Lister, 1976; Pianka, 1986). Despite some divergence in habitat selection along the dimensions of vegetation rank and perch height, discriminate analysis resulted in few significant differences between classes (i.e., niches, Table 4). Discrimination of a unique habitat niche for male *A. cybotes* was almost non-existent; 90% of the sample was misclassified as belonging to the other three species-sex niches (Table 5). Male *A. cybotes* occupied the central habitat position, both in terms of perch height and canonical variables



(Fig. 5), and their distribution was statistically indistinguishable from those of their neighbors.

We hypothesized that if interspecific aggression was having an effect on micro-distribution, it should be more intense in June than in November. This is because territorial behavior is enhanced during the breeding season (Stamps and Crews, 1976; Stamps, 1977). This aggression could manifest itself in decreased habitat niche overlap during June. However, we found no such evidence for interspecific territoriality as reported for some sympatric anoles (reviewed in references of the introduction).

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