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NICHE STRUCTURE OF AN ANOLE COMMUNITY IN A TROPICAL RAIN
FOREST WITHIN THE CHOCO REGION OF COLOMBIA

DISSERTATION

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By

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LCF

Castro-H, Fernando, Niche Structure of an Anole Community in a Tropical Rain Forest within the Choco Region of Colombia. Doctor of Philosophy (Biology), May, 1988, 107 pp., 20 tables, 10 figures, 13 Plates, bibliography, 81 titles.

Ten species of anoles at Bajo Calima within the Choco of western Colombia separate into two principal macrohabitat groups: (1) forest species (A. latifrons, A. chocorum, A. macrolepis, A. granuliceps, A. anchicayae and A. lyra), and (2) those inhabiting openings and edges (A. maculiventris, A. chloris, A. biporcatus and A. notopholis). The 10 anoles further separate according to ground and vegetation dwellers: A. granuliceps, A. notopholis and A. macrolepis (the latter being a semiaquatic species); and A. latifrons, A. chocorum, A. anchicayae, A. biporcatus, A. chloris, A. lyra and A. maculiventris, respectively. There is a relation at Bajo Calima between the number of anole species and vegetational structural diversity. Anole diversity within a given macrohabitat is by perch microsite/microclimate heterogeneity. These are the two major ecological dimensions along which similarity is limited or resources are partitioned. Pattern of anole body size and perch microsite preference at Bajo Calima is

similar to that on the Greater Antilles. Except in disturbed cultivated areas, no two anoles having similar body sizes share the same perch microsite within a macrohabitat. In cultivated areas the two more opportunistic species, A. chloris and A. anchicayae, overlap in microsite, but segregate slightly in size and microclimate preference. No taxonomic prey preference is indicated among the most common arthropods in the anoles' diets. However, prey size range differs among anoles and is related to anole snout-vent length. Interspecific competition among anoles at Bajo Calima for prey, if it occurs, should be asymmetrical. Current interspecific competition at Bajo Calima is not evident because of macrohabitat and perch microsite/microclimate structural segregation, and/or body size-prey size preference.

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CHAPTER I

INTRODUCTION

Anolis is the largest lizard genus in the new world, containing 200 known species distributed from the southern United States, throughout the Caribbean Islands, Central America and tropical South America. The systematics, behavior, ecology, biogeography, and evolution of many of these species have been studied intensively, particularly in the Greater and Lesser Antilles (e.g., Arnold, 1966; Collete, 1961; Fretwell, 1981; Gorman, et al., 1980; Hertz, 1976; Huey et al., 1976; Jenssen, 1977, 1981; Lazell, 1962, 1964, 1966, 1972; Lister, 1976; Moermond, 1977, 1979; Rand, 1964, 1967, 1969; Rand and Williams, 1969; Roughgarden, et al., 1983; Schoener, 1969, 1970a, 1970b, 1974, 1975; Schoener and Schoener, 1971a, 1971b; Williams and Rand, 1969; among others). Less work has been done with Central America Anolis (e.g., Andrews, 1971, 1979; Crump, 1971; Fitch, 1975; Guyer and Savage, 1987; Heatwole and Sexton, 1966; Heyer, 1967; Scott, 1976; Sexton and Turner, 1971 among others), and far less with those in South America (e.g., Ayala and Castro, in prep.; Dixon and Soini, 1975; Duellman, 1978, 1979; Rand and Humphrey, 1968; Vanzolini and Williams, 1970).

Studies on Anolis have provided insight into niche partitioning, competition, adaptive radiation, community structure and insular biogeography. Considerable theory and tests for hypotheses have derived from the Caribbean Island studies. Several comparative studies on mainland species have been conducted (Andrews, 1971, 1979; Fitch, 1975; Heatwole and Sexton, 1966; Pounds, in prep.; Williams and Rand, 1977), but more are needed to test hypotheses concerning expected differences between mainland and island lizard communities. This especially is true for tropical South America.

The Choco region on the Pacific coast of Colombia (Figure 1) is an excellent area for comparative studies of anoles. It supports a high diversity (ca. 25; Table I) apparently representing Anolis lines from the southern and northern hemispheres (Anolis alpha and beta species, respectively; Etheridge, 1960). The Choco appears to be the biogeographical confluence for and shows the highest diversity of Anolis alpha and beta species. The Choco is comprised of ca. 89,497 km² of lowlands, bounded by a branch of the Andes to the east (elevation ca. 3000 m), the Pacific Ocean to the west, a sub-xeric zone with some dry forests to the south and Panama Isthmus with low mountains to the North. It is essentially a "biogeographical island" (Plate I) on South American continent which provides the

TABLE I
 KNOWN LOWLAND (a) ANOLE SPECIES FROM THE CHOCO REGION

Section (b)(c)	Natural group	Species	Choco zone(d)		
			South	Middle	North
beta	Lionotus	<u>rivalis</u>	-	-	+
"	"	<u>poecilonotus</u>	-	-	+
"	Lemurinus	<u>vittigerus</u>	-	-	+
"	Pentaprion	<u>pentaprion</u>	-	-	+
"	?	<u>vicarius</u>	-	-	+
alpha	Latifrons	<u>frenatus</u>	-	-	+
"	"	<u>purpurescen</u>	-	-	+
"	Aequatorialis	<u>maculigula</u>	-	-	+
"	"	<u>mirus</u>	-	+	>>+
beta	Humilis	<u>notopholis</u>	-	+	>+
alfa	Punctatus	<u>anchicayae</u>	-	+	+
"	"	<u>chocorum</u>	+<	+	+
beta	Biporcatus	<u>biporcatus</u>	+	+	+
"	Fuscoauratus	<u>gracilipis</u>	+	+	+
"	"	<u>maculiventris</u>	+	+	+
alpha	Punctatus	<u>chloris</u>	+	+	+
beta	?	<u>granuliceps</u>	+	+	+
"	Lionotis	<u>macrolepis</u>	-	+	-
"	Lemurinus	<u>lyra</u>	+	+	-
alpha	Latifrons	<u>latifrons</u>	+<<	+	-
"	"	<u>princeps</u>	+	-	-
"	Punctatus	<u>peraccae</u>	+	-	-

(a) < 1000 m. (b) Section corresponds to Etheridge's (1960) division of the genus. (c) Natural groups follows Williams (1976) pattern as modified by Ayala and Castro (in prep.). (d) Three principal zones in which anoles are present (+) or absence (-).

opportunity to study anoline diversity and resource-partitioning without complications of elevational heterogeneity seen on the Caribbean Islands (Table II).

Figure 1. Map of Colombia showing the Choco Region (shaded area) and The Bajo Calima study site.



TABLE II
COMPARISON OF CHOCO REGION AND CARIBBEAN ISLANDS

The number of island species are from Williams (1982). The alpha and beta correspond to Etheridge's (1960) division of the anole genus, (+) present; (-) absence. The topography represents an inclusion of mountains over 1000 m. Area is given in km². the species/area estimates are per 1000 km².

Place	#species	alpha	beta	Area	spp./area	Topography
Cuba	28	+	+	110,922	2.5	mountainous
Hispaniola	23	+	+	72,415	3.2	mountainous
Puerto Rico	11	+	+	8,897	12.4	mountainous
Jamaica	7	-	+	10,962	6.4	mountainous
Choco Region	23	+	+	89,454	2.6	lowland

The study presented herein is the first phase of a long-term extensive project on the ecology, evolution and biogeography of anoles in the Choco of Colombia. I focus on the Choco because of its biogeographic significance, high diversity of sympatric species of anoles and personal familiarity with the region. My long-term objectives are to circumscribe the anole community in terms accordant with the principal Caribbean Island and Central America studies (e.g., Andrews, 1971, 1976, 1979; Heckel and Roughgarden, 1979; Rand, 1961, 1962, 1964, 1967; Roughgarden, 1974; Roughgarden, et al., 1983; Schoener, 1968, 1970a, 1970b, 1974a, 1974b, 1975; Schoener and Schoener, 1971a, 1971b, 1980; Williams, 1963a, 1968, 1969, 1972, 1976, 1977, 1983)

for direct comparison between the Choco, a mainland "island," with those in the Caribbean.

Since a major determinant of community diversity is the way in which coexisting species partition resources among themselves (Pianka, 1974), my investigation focused on spatial and trophic resource partitioning by 10 species of anoles. Specifically, my objective was to describe utilization of macrohabitat (primary forest, secondary forest, open forest and cultivated areas), microhabitats (perch microsites: surface, shrubs and trees, and heights: 0, 0 - 2, 2 - 5 and > 5 m), microclimates (sunny, partially sunny and shaded) and diets (operational invertebrate taxonomic units, OTUs, and the volume diversity). I was interested in assessing overall niche breadth and overlap among the 10 species along the spatial, microclimatic and trophic dimensions.

Plate I. Topographic map of western Colombia showing isolation of the Choco Region by The Andean Mountains. Bajo Calima study site is indicated by red dot.



Plate II. Aerial photograph of primary forest at the Bajo Calima study site showing effects of logging.



Plate III. Aerial photographs of the Bajo Calima study site showing agricultural effects along the Calima River and roads (top), and logging effects (bottom) on forests.

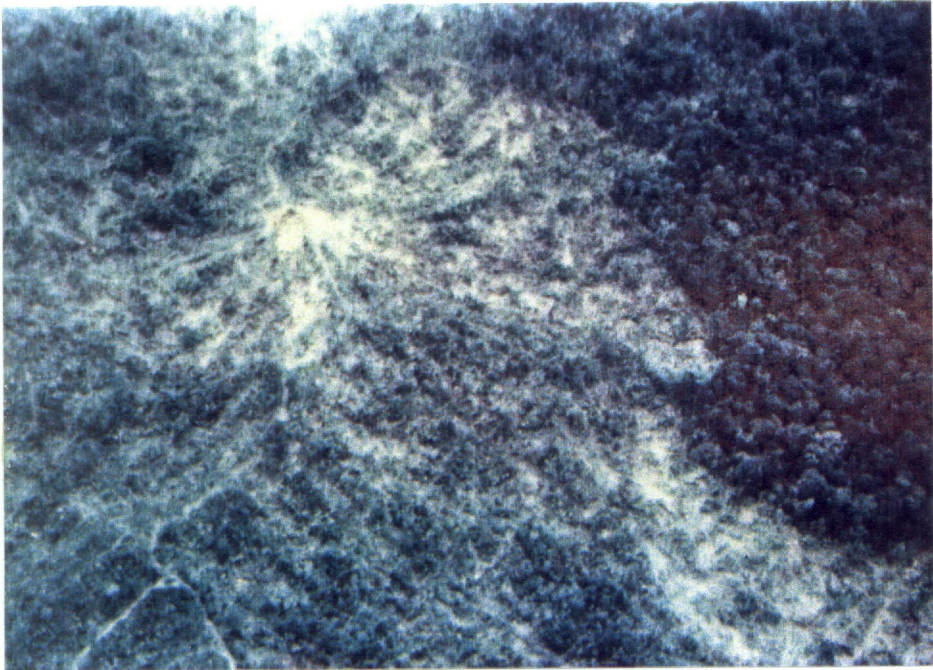


Figure 2. Temperature and relative humidity at The Bajo Calima study site.

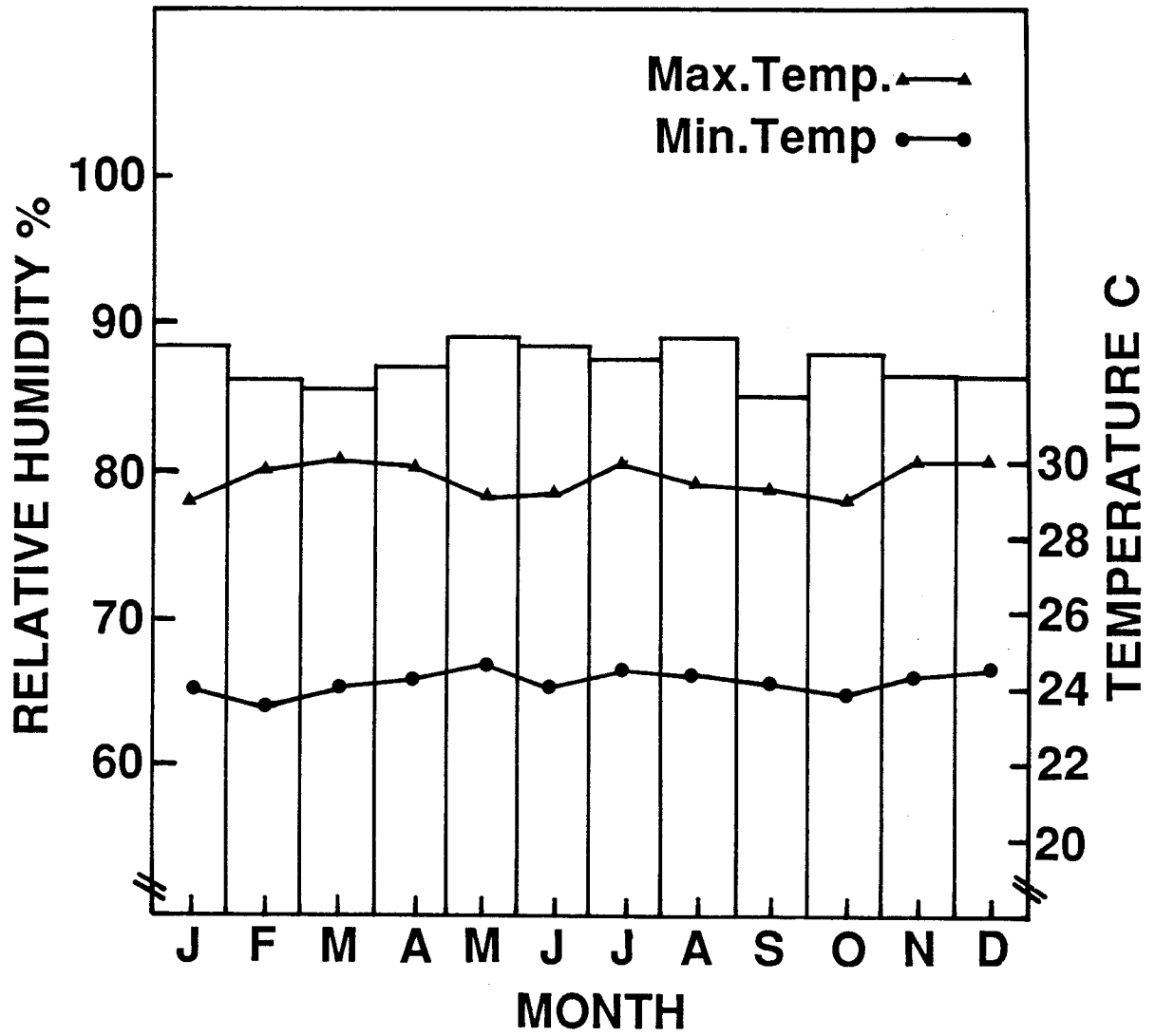
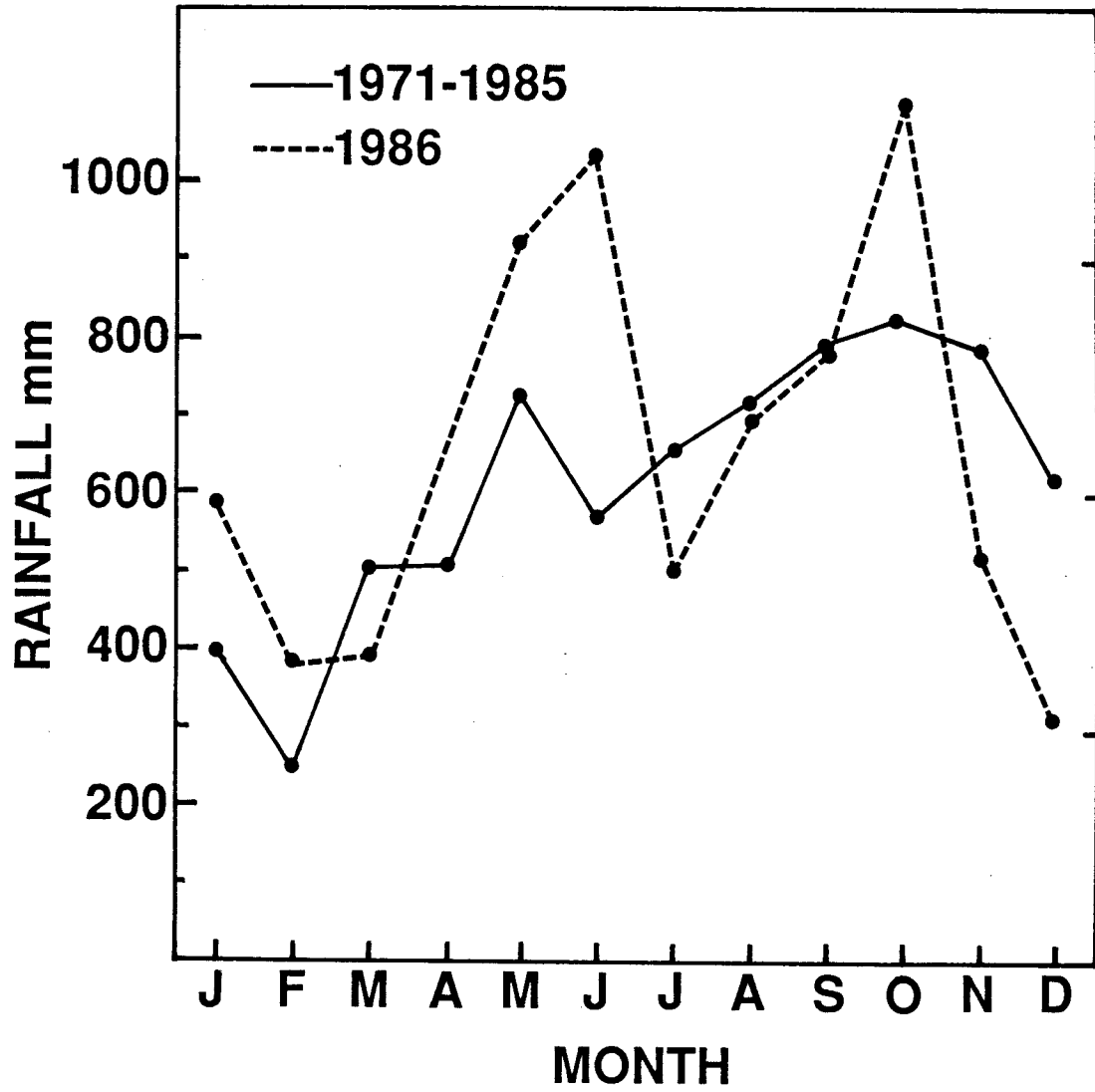


Figure 3. Monthly rainfall at the Bajo Calima study site.



CHAPTER II

STUDY SITE

The specific area where the study was conducted is called Bajo Calima ($3^{\circ} 59' N$ $76^{\circ} 56' W$), located 30 km North of Buenaventura (Figure 1; Plate I). The elevation is approximately 100-m above sea level. The climate is typical for tropical rainforests on the Pacific coast of Colombia. Table III contains climatic data for 1971 - 1986. Mean (\pm SD) annual and monthly rainfall are 7369 ± 990 and 611 ± 87.8 mm, respectively, for that period. Rain falls an average of $300 (\pm 26)$ days per year, but is heaviest during July and September-October (Figure 2). Minimal and maximal temperatures average 23.8 and 29.7 C. Relative humidity is nearly constant (ca. 87 percent) throughout the year. During 1986, when most of the study was conducted, there were 315 days of rain for a total of 7870 mm (monthly average 612 ± 64 mm). Mean minimal and maximal temperatures were 24.2 and 29.6 C, respectively (Figures 2 - 3).

The vegetation of Bajo Calima is well described by Gentry (1982, 1986) and Richards (1982). According to Gentry (1986), the primary forest in Bajo Calima is the most diverse in the entire region, and correlated with its high rainfall. The area was covered by primary forests (Plate II)

TABLE III
METEOROLOGICAL CHARACTERIZATION OF BAJO CALIMA(a)

Year	Days of rain	Rainfall mm		Temperature C	
		annual	\bar{X} month	minimum	maximum
1971	245	6991	582.6	22.99	29.1
1972	269	5798	438.2	23.84	30.63
1973	250	7295	607.2	23.83	30.00
1974	301	7835	653.0	23.44	29.50
1975	322	8662	721.9	23.48	29.18
1976	301	6210	517.5	23.81	29.21
1977	294	8355	696.3	24.13	29.22
1978	316	8339	694.9	23.88	29.42
1979	313	8407	700.6	23.95	29.74
1980	322	7014	584.5	24.00	29.82
1981	337	8698	724.8	23.76	29.73
1982	297	5964	496.9	24.15	30.19
1983	313	6068	505.7	25.00	30.72
1984	291	7196	599.3	23.66	29.70
1985	314	7200	609.4	24.20	29.80
1986	315	7870	655.8	24.20	29.60
\bar{X}	300	7369	611.8	23.90	29.70
SD	25.8	990	87.8	0.43	0.48

(a). Data from Pulpapel S.A. (HIMAT) station

with the exceptions of small man-made clearings along the rivers until few years ago when human cultivation and logging activities increased (Plates II -III). At present, Bajo Calima vegetation can be divided into four functional types: (1) primary forest; (2) secondary forest; (3) open forest; and (4) cultivated zones.

The primary forest (Plates IV - V) is characterized by a nearly continuous canopy and relatively deep organically rich soil. The most dense vegetation occurs on high areas known as colinas bajas. These are drained by runoff and not flooded. Less dense vegetation occurs in lower areas called bajiales or guandales (Armando Vasquez, pers. comm.) which are flooded during periods of heavy rain. The canopy formed by the largest small-leaf trees is 30 - 35 m above ground. Those trees have extensive buttresses which extend 2 - 3 m along the trunks. A secondary stratum, 15 - 20 m above the ground, usually consists of broad-leaf trees with wide buttresses, and stilt palms. A lower layer 8 - 12 m high, which consists smaller broad-leaf trees and spiny palms, represents renewal growth.

The vegetation on guandales near the surface is of diverse broad-leaf herbs under 1 m tall. The soil is shallow, 5 - 10 cm of leaf litter which decomposes rapidly because of the wet conditions. Trees have extensive shallow horizontal roots which allow for exploitation of the nutrients within the thin soil. As a result of being shallow-rooted, the larger trees are often blown-over during the infrequent heavy thunderstorms at Bajo Calima. Felled trees produce natural clearings in the middle of the forest, which are characterized by successional plant species of shrubs, weeds and opportunists such as Cecropia

spp. and several Melastomatceae plants which reach 10 - 12 m in height. Both man-made and natural clearings are quickly grown over by these successional plants.

Lianas are numerous in the primary forest, as are heavy growths of epiphytes (e.g., bromeliads, ferns, mosses and orchids) along the horizontal branches of trees. Bromeliads are very common and important for faunal diversity. They produce a high diversity of microclimatic habitats, increasing spatial niches throughout the primary forests.

The secondary forest (Plates V - VI) is actually an advanced successional stage, consisting of dense bushy undergrowth, some trees, few lianas and herbs, and shallow leaf litter. Trees are represented by small individual belonging to the Rubiaceae, Anonaceae, Melastomataceae, Moraceae, Apocynaceae, Burceraceae, Guttiferae, Mimosaceae, Ochnaceae, Rutaceae, Sapindaceae, Sapotaceae, Tiliaceae and Ulmaceae, which were not cut during logging activities.

The edges of primary and secondary forests are characterized by extremely dense growths of leafy successional vines which form an almost impenetrable vegetational matrix. Within the forests are small streams and drainage areas with aquatic plants such as Heliconies (Heliconeae).

Open forests (Plate VI - VII) contain recently cleared areas which are undergoing early succession. Some common

families of plants are, Brossimum utile (Moraceae), Visnia ferruginea and V. ruffa (Miristicaceae), Bochyciaceae, Rutaceae, Fabaceae, Ciperaceae, Mimosaceae, and Rubiacea. Between clearings and the forests are ecotones containing Gleichesiiaceae (ferns), Musaceae (banana plants), Zingiberaceae (Costus spp.) and others fruit bushes and palms. Frequently, cleared areas are cultivated with Yuca, papa-china, pineapple, platano and banana.

Plate IV. Ground level views of primary forest at The Bajo Calima study site.



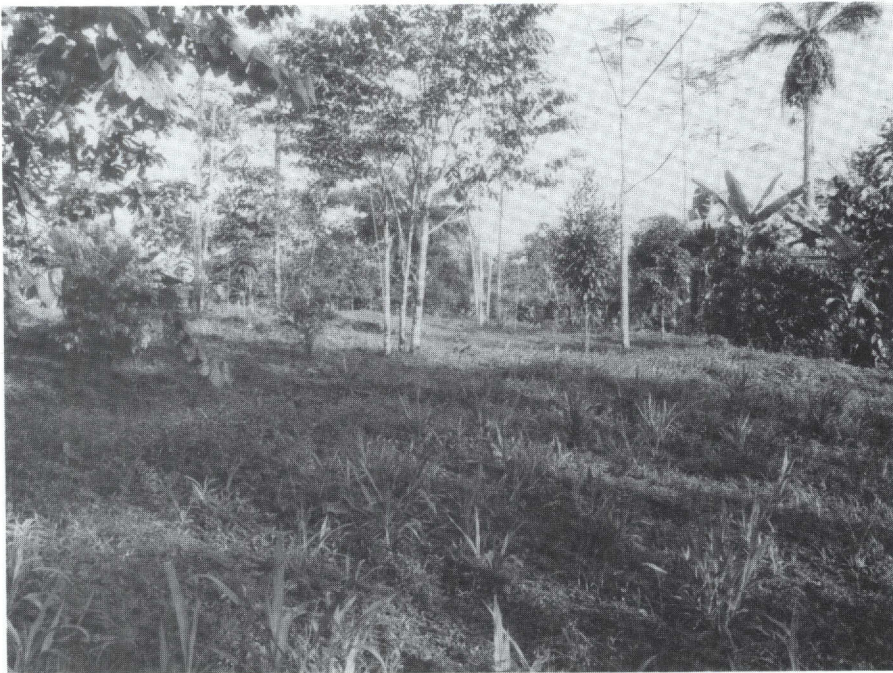
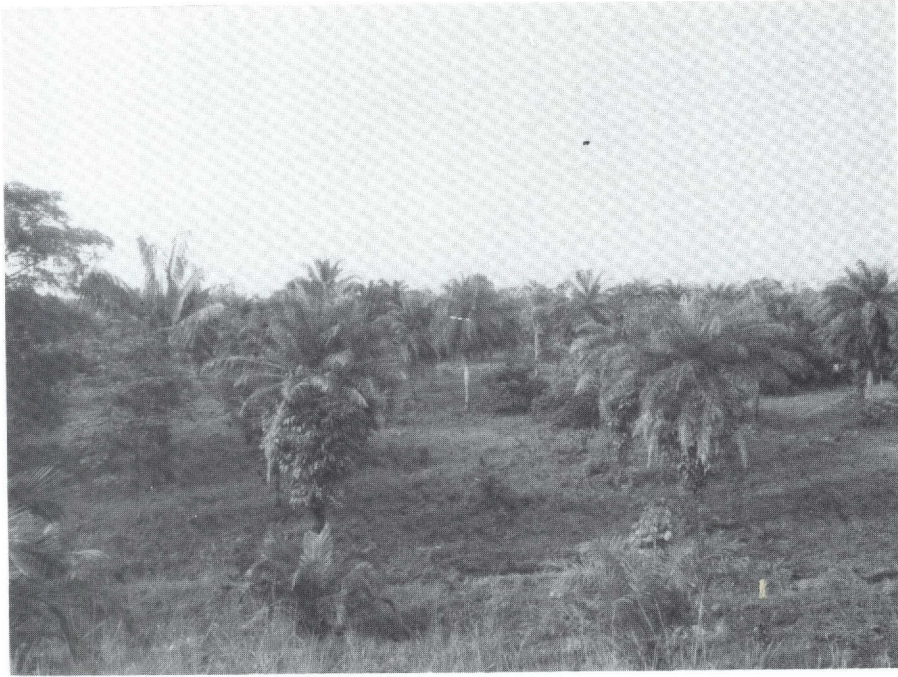
Plate V. Ground level views of primary forest showing a stream (bottom) covered with palms.



Plate VI. Ground level view of secondary (top) and open (bottom) forests at The Bajo Calima study site.



Plate VII. Ground level views of cleared areas used for cultivation of African oil palms (top) and fruit trees (bottom)



CHAPTER III

SPECIES STUDIED

Of the 200 known species of Anolis, over 10 percent are found in the Choco (Table I), the highest diversity in the Neotropics. Within the 5000 ha surveyed in Bajo Calima, I observed 12 species (Table IV). Of those, I selected the 10 most abundant for the current study. These are described below.

Anolis granuliceps.--(Plate VIII). Small size, having a maximal snout-vent length (SVL) of 49 mm. Color is dark brown. With the exception of some small black spots, there is distinct dorsal pattern. Four dark brown lateral stripes extend from the head to base of tail. Color and pattern are relatively fixed characteristics. Males have a very small dewlap with small yellow extensions containing white scales. Legs are relatively large for the body length.

A. macrolepis.--(Plate VIII). Small to medium size with maximal SVL of 60 mm. Color grayish with large lateral band, bordered on the underside by a narrow distinct whitish line and some chevrons above. The venter is whitish. Color and pattern are stable. Only males have dewlaps, which are yellow with some small white scales. Legs are relatively large to the SVL.

TABLE IV
 ANOLE LIZARD COMMUNITY AT BAJO CALIMA

Natural group (a)	Species	Maximum SVL mm	Basic color (b)	Common pattern	Perch
Latifrons	<u>latifrons</u>	131.0	green/brown	spotted	crown
Punctatus	<u>chocorum</u>	80.0	green	striped	trunk
"	<u>anchicayae</u>	56.0	green/brown	homogen	twig
"	<u>chloris</u>	55.0	green	spotted	leaves
Biporcat.	<u>biporcatus</u>	100.0	green/brown	homogen	trunk
Lemurinu.	<u>lyra</u>	70.0	green	homogen	leaves
Lionotus	<u>macrolepis</u>	60.0	green	homogen	bushes
Fuscoaurat.	<u>gracilipes</u> (c)	55.0	brown/yellow	blocks	bushes
"	<u>maculiventr.</u>	48.0	grey/yellow	striped	ground
Humilis	<u>notopholis</u>	51.0	brown/green	blocks	semi-
?	<u>granuliceps</u>	55.0	brown/green	striped	aquatic
?	new spp.(c)	45.0	brown	homogen	ground
				bicolor	herbs
				homogen	bushes
				chevron	trunk
				bicolor	ground
				striped	herbs
				spotted	ground
					shrub

(a) Natural groups following Williams (1976). (b) Basic color primary/secondary. (c) Reported as species but very rare.

A. anchicayae.--(Plate IX). Small to medium size with maximal SVL of 56 mm. Sexes differ slightly in color and pattern. Males have a striped dorsum with clear brown undulating borders. Numerous green spots, which can change

to light yellow, are on the dark sides. Females have a distinct mid-dorsal stripe. Laterally, there is a narrow clear brown stripe and several green zones. Color and pattern are variable. Dewlaps, found only in males, are relatively large and pale yellow or clear green. Legs are relatively small for the body length.

A. chloris.--(Plate IX). Small size with maximal SVL of 55 mm. Color is stable, homogeneously green dorso-laterally with a whitish venter. Dewlaps are in males only, relatively large and pale yellow. Legs are relatively short for the body size.

A. maculiventris.--(Plate X). Small with maximal SVL of 48 mm. There is a slight sexual dimorphism in color pattern. Males are homogeneous light brown with tiny black occipital spot. Females often have a tan or whitish mid-dorsal stripe with dark brown edges. Color and pattern are not stable. Only males have dewlaps, which are medium sized with pink- red color skin and few yellow scales. Legs are relatively long.

A. latifrons.--(Plate X). Large size, maximal SVL of 131 mm. Color is basically green with a stable dorso-lateral pattern of diagonal dark-black stripes. There is a conspicuous black spot with a white center on a side of shoulders. Only males have dewlaps, which are pale yellow. Legs are long, relative to SVL.

A. chocorum.--(Plate XI). Medium to large size, with SVL of 80 mm. Color is homogeneous green with dark-light green bands frequently appearing dorso-laterally. Color pattern is not stable. Dewlaps are present in both sexes, but smaller in females. Color is orange and white with irregular pattern. Legs are relatively small.

A. biporcatus.--(Plate XII). Large with maximal SVL of 100 mm. Color is variable from homogeneous green with some reticular pattern to red-brown. Only males have dewlaps, which are very small. They are red or intense pink with some dark scales. Legs are relatively short.

A. notopholis.--(Plate XI). Small with maximal SVL of 50 mm. Color pattern is stable, with dark and pale brown mid-dorsal chevrons. The venter is pale green. Dewlaps are relatively small, with those in males slightly larger than females. Red color in the skin and yellow scales. Legs are large.

A. lyra.--(Plate XII). Medium size with maximal SVL of 70 mm. Color is yellow and brown. Only males have dewlaps, which are very small, of pink color with a dark spot in the middle. Legs are long.

Two other species have been found within the study area; A. gracilipes and a new species (Plate XIII) which is being studied by E. E. Williams (pers. comm.) (Plate XIII).

Plate VIII. Anolis granuliceps (top) and Anolis macrolepis
(bottom).



Plate XIX. Anolis anchicayae (top) and Anolis chloris
(bottom)



Plate X. Anolis maculiventris (top) and Anolis latifrons
(bottom).

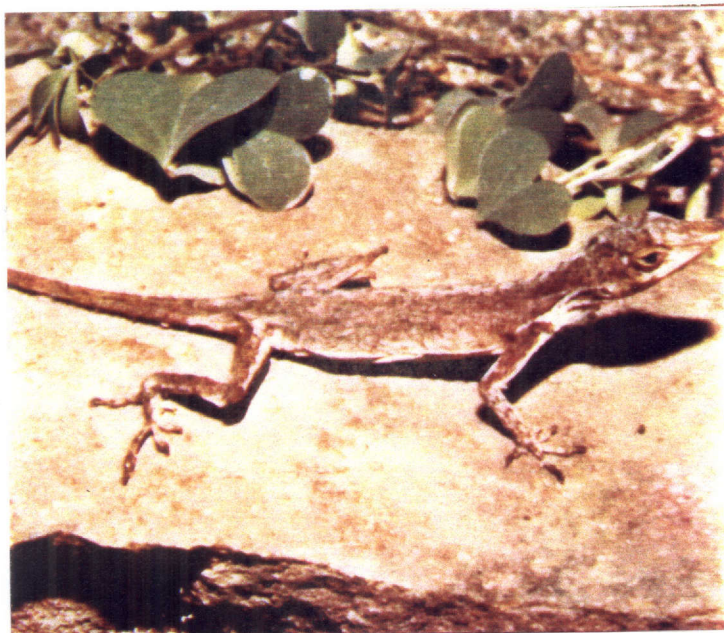


Plate XI. Anolis chocorum (top) and Anolis biporcatus
(bottom).



Plate XII. Anolis notopholis (top) and Anolis lyra
(bottom).

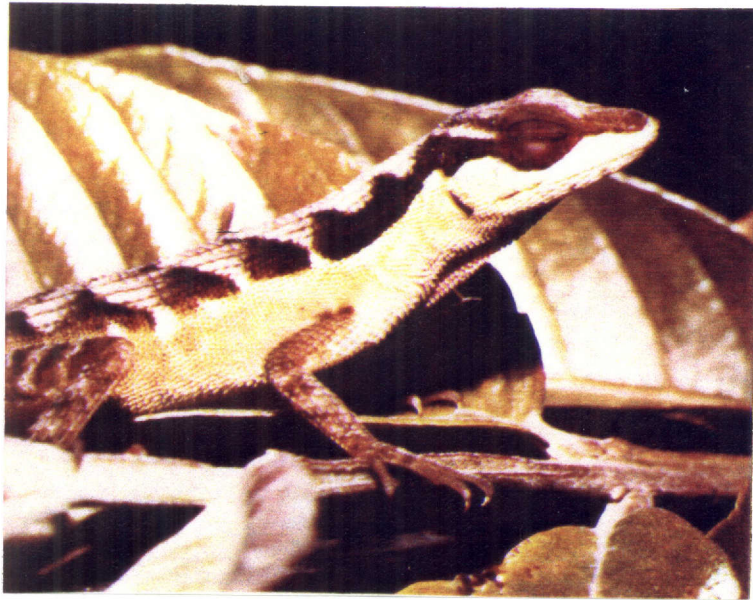


Plate XIII. New species of Anolis (top) and Anolis
gracilipes (bottom). Both species are rare on the study
site.



CHAPTER IV

METHODS

Since my work is the first ecological study of anoles in Bajo Calima, many basic techniques had to be modified from those used elsewhere, especially in the Caribbean (Schoener 1968, 1970a, 1974; Roughgarden et al. 1983; Rand 1964). The major objectives were to: (1) survey four macrohabitat divisions (primary, secondary, and open forests, and cultivated areas) and determine the relative frequencies of each species among them; (2) describe the perch preferences or relative frequencies of each species among various perch categories on the surface and vegetation; (3) assess microclimate preference along a sunny-partially sunny-shaded continuum; (4) determine general dietary pattern among the species; and (5) describe the primary morphological characters of each species. Species were indentified according to Ayala and Castro (In prep.) with nomenclature from Williams (1976). Meteorological data during December 1985 - December 1986 were collected on-site. Data prior to my study came from records of the weather station at Pulpapel S.A. (HIMAT) located 5 km from the site and Gonzales (1984).

Macrohabitat Dispersion

I established a 100- x 200-m plot in each of the four macrohabitats. Each was subdivided into four 50- x 100-m sections and one was selected at random for intensive observations. A 1-m path was cut around each subplot to facilitate surveying. Each study plot was surveyed during the anoles activity period (0830 - 1530 h) on 158 separate days and each anole observed was recorded according to specific location within the macrohabitat subplot.

Abundance

Abundance is extremely difficult to determine in a complex tropical rainforest for anoles, which vary greatly in behavior, crypsis, actual density and microhabitat preference, both among themselves and among macrohabitats. I chose to use the original Schumacher and Eschmeyer (1943) multiple-mark recapture method because of ease in use (relative to modification by Blower, Cook and bishop (1981)). I marked all anoles, except A. macrolepis, with paint discharged from a forester's paint gun at distances of 2 - 4 m. Usually, marks were near the juncture of tail and rear legs. A. macrolepis was hand-captured and marked with enamel paint because of its semiaquatic preference. Each mark-recapture assessment was made on four consecutive days. Species were studied only in the macrohabitat where they appeared to be more frequent and conducive to enumeration.

A. chocorum was not included because it exists in the high canopy and could not be marked.

Microhabitat Dispersion

Although Rand (1968) points out that anoles separate structurally according to perch height and diameter (i.e., trunk, branch), I used only perch height and microclimate. This was because of the low absolute sample sizes and extensive complexity of the vegetation at Bajo Calima which appears to exceed that in the Caribbean Island. The principal perch preference categories are: (1) surface, both terrestrial and confines of streams; (2) shrubs 0 - 2 m; (3) trees 0 - 2 m; (4) trees 2 - 5 m; and trees > 5 m. Each anole observed during the study was recorded according to those locations, and additionally as to whether it was in full sun (sunny perch), partial sun or shade, the major microclimatic preferences of anoles (Williams, 1983; Rand, 1967).

Dietary Preference

Diets were assessed by examining stomach contents of anoles collected outside the study plots from nearly identical habitats. Stomach contents were divided into operational taxonomic units (OTUs; Dunham, 1983) based principally on ordinal levels, with the volume of each prey determined following Dunham (1983) with the relation

$$V = 4/3 \pi (a/2)(b/2)^2, \quad (1)$$

in which a= longitudinal dimension or length and b= width. Data from field-collected anoles were augmented with museum specimens, especially for those anoles difficult to collect (e.g., A. chocorum and A. biporcatus). Museum specimens were from the same general area as Bajo Calima with similar habitat, topography, and elevation (e.g., Malaga and Buenaventura). Taxonomic identification was through comparison with the entomological collection and material revised by Maria R. Manzano at the Universidad del Valle, Cali, Colombia.

Morphometrics

The following principal measurements were taken, to 0.1 mm, on both freshly-collected adult anoles and museum specimens to assess possible relations: (1) snout-vent length (SVL); (2) head length (HL) from tip of snout to edge of occipital depression; (3) head depth (HD) at level of eyes; (4) head width (HW) posterior to eyes; (5) length of maxilla (MAX); (6) right femur length (FM) from insertion to outside edge of the knee; (7) right tibia length (PER) from knee to the foot articulation; (8) right hind limb (TB); and (9) right foot length (FT) from tip of fourth toe to the articulation with the tibia. Independent t-tests were used to determine size differences between anoles.

Data Analysis

Niche breadth along each of the principal dimensions (macrohabitat, perch, microclimate and diet) is calculated for the anoles using the Shannon-Wiener index (Colwell and Futuyama, 1971; Zar, 1984), which accounts for both richness or diversity of resource-states used and the relative frequency or equitability of their use. The index, B' , is calculated with the equation

$$B' = - \sum_{j=1}^N p_{ij} \log p_{ij} , \quad (2)$$

where p_{ij} is the relative frequency of the i th species of anoles using the j th of N resources. For macrohabitat niche breadth, $N=4$ (primary forest, secondary forest, open forest and cultivated area) and p_{ij} is the relative frequency of the total observations of an anole species made within each of the four macrohabitats. Products of the relative frequencies and their respective logarithms are summed to produce the niche breadth measure B' . For perch microsite and microclimate, $N=5$ (terrestrial surface; and stream surface; shrubs 0 - 2 m; and trees 0 - 2 m, 2 - 5 m, > 5 m) and $N=3$ (sunny, partially sunny and shaded), respectively. Since niche breadth for diet is determined for OTUs (i.e., ordinal classification) and volume diversity of prey, N varies.

Maximal niche breadth (B_{max}) obtains when a species utilizes all resource states in equal frequency. For macrohabitat as an example, B_{max} would occur when a species is dispersed with equal frequency (0.25) among primary, secondary, and open forests, and cultivated areas. Calculation of the equitability or evenness (E) component of B' is with the relation

$$E = B' / B_{max} , \quad (3)$$

where B_{max} is the $\log N$ (the number of resource states).

Niche overlap or similarity between species is calculated using the Colwell and Futuyama (1971) equation

$$C = 1 - 1/2 \sum |p_{ij} - p_{hj}| , \quad (4)$$

Where p_{ij} is the proportion of species i which utilizes resource category j , and p_{hj} is the proportion of species h utilizing the same resource. This procedure results in a matrix of species-by-species percentage overlaps. To further analyze overlap the "unweighted pair-group method using arithmetic average" (UPGMA), first used in numerical taxonomy (Sneath and Sokal, 1973), was employed to cluster the anole species according to their resource utilization similarity in phenograms (see Crisci and Lopez, 1983 for description of the method, and Duellman, 1978 for use with herps). Anoles utilizing resources in similar ways segregate

or cluster according to the percentage of similarity (i.e. "similarity distance").

Comparison of macrohabitats in terms of anole similarity is calculated with the Whittaker (1970) coefficient of community similarity:

$$CC = S_{ab} / (S_a + S_b - S_{ab}) , \quad (5)$$

where S_{ab} is the number of anole species shared by communities (macrohabitats) A and B, S_a is the total number of anole species present in macrohabitat A and S_b is the number present in macrohabitat B. Macrohabitats are clustered using the UPGMA procedure to relate their similarity according to anole species presence.

The Kolmogorov-Smirnov goodness of fit test (Zar, 1984) is used to test whether each species exploits a given resource dimension randomly (null hypothesis). Macrohabitat, perch microsite and microclimate are all niche dimensions which can be ordered. Macrohabitat is ordered as primary forest, secondary forest, open forest and cultivated areas based on successional stages and decreasing structure. Perch microsite is ordered from ground to the canopy and microclimate from sunny to shaded sites. Thus, the Kolmogorov-Smirnov test is appropriate for the analysis of these spatial dimensions. However since dietary items can not be ordered, the test is not used with the trophic dimension.

CHAPTER V

RESULTS

A total of 258 individuals belonging to 10 species of Anolis were observed during December 1985 to November 1986 within the 5000 ha study site, which included primary forest (ca. 50 percent), secondary forest (ca. 20 percent), open forest (ca. 10 percent) and cultivated area (ca. 20 percent). Following is a description of the dispersion of anoles among and within macrohabitat, microhabitat, microclimate preference, and their dietary patterns.

Macrohabitat Dispersion

Tables V - VI and Figures 4 - 5 provide information on niche breadth and overlap or similarity, relative abundance and diversity of the 10 Anolis spp. Using the Shannon-Wiener index (eq. 2) as a measure of macrohabitat niche breadth (B'), the 10 species are ranked in decreasing order in Table V. B' reflects both the number of macrohabitats occupied, and the relative frequency of occurrence or equitability. Table V contains absolute number and frequency of observations for each anole species. A. anchicayae has the widest macrohabitat dispersion (four) and highest B'. Six species are found in three macrohabitats and three are restricted to two. The hypothesis that a given species is

TABLE V
MACROHABITAT DISPERSION

Number and relative frequency of 10 anole species among macrohabitats. B' = niche breadth calculated with the Shannon-Weiner index. Dmax = maximal difference value of the Kolmogorov-Smirnov goodness of fit test; those with asterisk are significant at 5 percent. n, total lizard observations.

Species	n	Primary forest	Secondary forest	Open forest	Cultivated zone	B'	Dmax
<u>anchicayae</u>	48	17 (.35)	17 (.35)	6 (.13)	8 (.17)	.56	10.0*
<u>lyra</u>	22	4 (.18)	12 (.55)	6 (.27)	0 (.00)	.43	5.5
<u>maculivent.</u>	36	0 (.00)	9 (.25)	20 (.56)	7 (.19)	.43	9.0*
<u>granuliceps</u>	31	18 (.58)	11 (.36)	2 (.06)	0 (.00)	.37	13.5*
<u>notopholis</u>	31	0 (.00)	1 (.03)	12 (.39)	18 (.58)	.35	14.5*
<u>chloris</u>	35	0 (.00)	1 (.03)	15 (.43)	19 (.54)	.35	16.5*
<u>biporcatus</u>	8	0 (.00)	1 (.13)	6 (.74)	1 (.13)	.32	3.0
<u>latifrons</u>	21	16 (.76)	5 (.24)	0 (.00)	0 (.00)	.24	10.8*
<u>chocorum</u>	10	2 (.20)	8 (.80)	0 (.00)	0 (.00)	.22	5.0*
<u>macrolepis</u>	16	13 (.81)	3 (.19)	0 (.00)	0 (.00)	.21	9.0*

randomly dispersed among the four macrohabitats is rejected for all but A. lyra and A. biporcatus, using the Kolmogorov-Smirnov goodness of fit test for discrete data at level of 5 percent significance (Zar, 1984). The small sample size for A. biporcatus, an extremely cryptic and rare anole, obscures its pattern of being an open forest inhabitant. A. lyra is basically a forest species, but frequents edges.

Figure 4 is a dendrogram graphically illustrating overlap or similarity in macrohabitat utilization of each

TABLE VI
MACROHABITAT NICHE OVERLAP

Similarity of 10 anole species as percent overlap calculated following Colwell and Futuyama (1971).

Species	A	B	C	D	E	F	G	H	I	J
A <u>granuliceps</u>	1.0
B <u>macrolepis</u>	.77	1.0
C <u>anchicayae</u>	.77	.54	1.0
D <u>chloris</u>	.03	.03	.03	1.0
E <u>maculiventris</u>	.32	.19	.72	.65	1.0
F <u>latifrons</u>	.82	.95	.59	.03	.24	1.0
G <u>chocorum</u>	.56	.39	.55	.03	.25	.03	1.0	.	.	.
H <u>notopholis</u>	.10	.03	.32	.96	.61	.03	.03	1.0	.	.
I <u>biporcatus</u>	.19	.13	.38	.58	.81	.13	.48	.54	1.0	.
J <u>lyra</u>	.60	.37	.66	.30	.52	.42	.73	.31	.40	1.0

species as compared to the others. Table VI is a matrix showing pair by pair percent overlap among species calculated with the Colwell and Futuyama (1971) method (eq. 4). Three principal groups emerge in Figure 4. Group one is composed of A. macrolepis, A. latifrons and A. granuliceps, anoles inhabiting the inner primary forest. In other words, they are key or characteristic species for undisturbed forest. Group two contains two subgroups. The first, composed of A. chocorum and A. lyra is found most frequently in secondary forests, but tending towards denser vegetation. A. chocorum is an upper canopy species and is more easily detected in secondary forests than within the closed canopy

Figure 4. Dendrogram of macrohabitat similarity among anoles at the Bajo Calima study site.

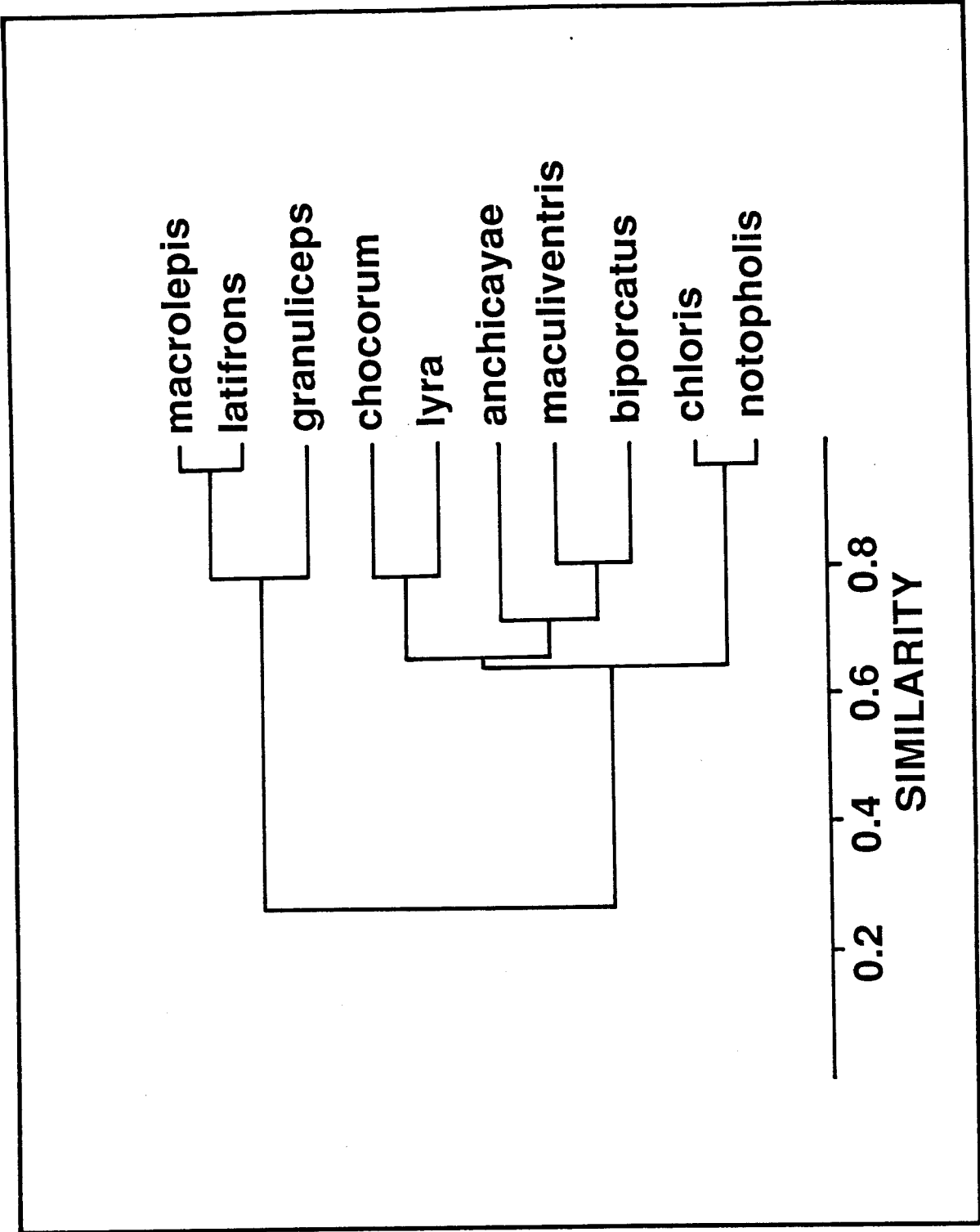


Figure 5. Community coefficient and similarity for principal macrohabitats at the Bajo Calima study site based on composition of anoles.

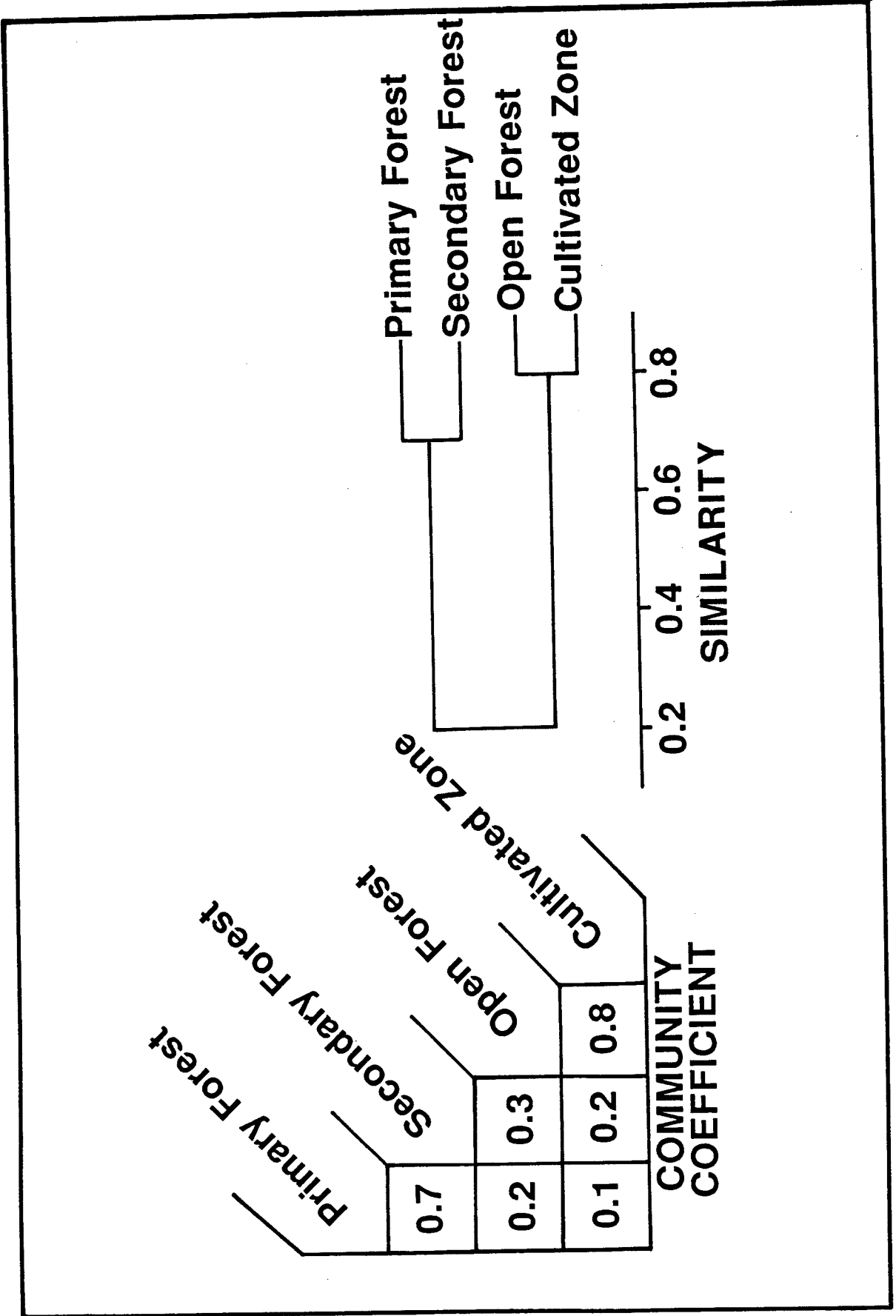
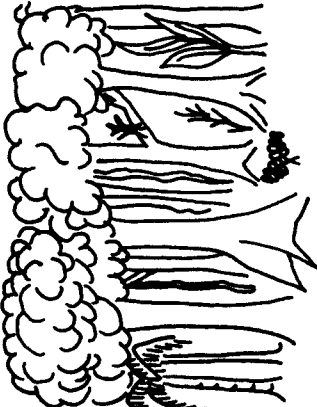
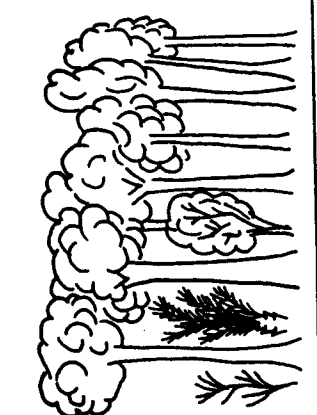
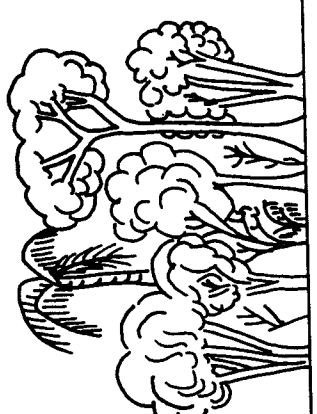
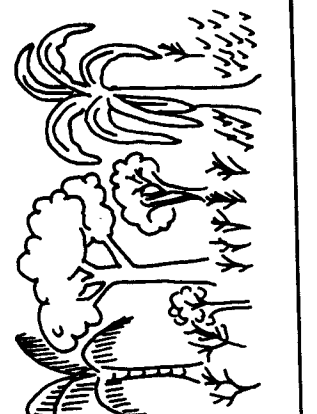


Figure 6. Profile of four principal macrohabitats and anole species distribution at the Bajo Calima study site.

Primary Forest	Secondary Forest	Open Forest	Cultivated Zone
			
<ul style="list-style-type: none"> * macrolepis * granuliceps * latifrons chocorum lyra anchicayae 	<ul style="list-style-type: none"> granuliceps latifrons * chocorum * lyra anchicayae maculiventris 	<ul style="list-style-type: none"> lyra anchicayae * maculiventris * chloris * biporcatus notopholis 	<ul style="list-style-type: none"> anchicayae maculiventris * chloris biporcatus * notopholis

of primary forests. The other, represented by A. anchicayae, A. maculiventris and A. biporcatus also frequent secondary forest, but more towards open areas. A. chloris and A. notopholis which form the third group, are most common in open areas and/or clearings, including cultivated areas.

The dendrogram in Figure 5 shows the similarity among macrohabitats based on their composition of 10 anole species. The matrix in Figure 5 gives the coefficient of similarity obtained by Whittaker method (Whittaker, 1970) and as used by Duellman (1978). Primary and secondary forest, and open forest and cultivated areas separate, respectively. Figure 6 is an illustration of the four macrohabitats, showing their key species (indicated with asterisk) and the overall dispersion of each anole species among them. Species diversity of each macrohabitat, measured as the number of species (s) is highest in the secondary forest (10), followed by open forest (6), primary forest (5) and cultivated zone (2). Use of other diversity indices (e.g., Shannon's H', Simpson's D) which integrate richness and evenness is not possible because of difficulties in assessing relative abundance of the anoles (see below).

Density estimates (Table VII), made using the Schumacher and Eschmeyer (1943) multiple mark-recapture method, are given for all but A. chocorum which inhabits the

TABLE VII

RELATIVE ABUNDANCE OF NINE ANOLE SPECIES

Relative abundance of nine(a) anole species at Bajo Calima within four macrohabitats. Number are densities per 50 x 50 m plots. Those in parentheses are per hectarea.

Species	Primary forest	Secondary forest	Open Forest	Cultivated zone
<u>granuliceps</u>	42 (168)	14 (56)	NA	NP
<u>macrolepis</u> (b)	17	NA	NP	NP
<u>anchicayae</u>	29 (114)	48 (191)	13 (54)	15 (60)
<u>chloris</u>	NP	26 (104)	40 (159)	39 (157)
<u>maculiventris</u>	NP	17 (68)	36 (145)	18 (70)
<u>latifrons</u>	11 (45)	13 (53)	NP	NP
<u>notopholis</u>	NP	NA	37 (147)	29 (120)
<u>biporcatus</u>	NP	NA	3 (11)	NA
<u>lyra</u>	NA	11 (43)	8 (33)	NP

(a) Anolis chocorum omitted because of difficulty in sampling within high canopy. (b) Only sampled along 200 m of stream. NA: no attempt. NP: not present.

upper canopy and is nearly impossible to effectively mark and recapture. Other species were not quantified in all macrohabitats because of absence or rarity. Since detectability varies among species and macrohabitats, density estimates are difficult to compare. Perhaps, density estimates are best used to detect changes in a given species among seasons/years within a given macrohabitat.

Microhabitat Dispersion

There are two principal dimensions for microhabitat segregation within each macrohabitat, perch microsite and microclimatic preference or microsite. The first is divided into surface (ground and stream) and vegetation. Vegetation is subdivided into shrub (0 - 2 m above surface) and tree, which is further divided by height (0 - 2, 2 - 5 and > 5 m above surface). Microclimatic preference refers to three positions in the sun-shade continuum: (1) sunny; (2) partially sunny; and (3) shade.

Tables VIII - IX and Figure 7 contain perch microsites data for the 10 species. Niche breadth in terms of perch microsite measured by the Shannon-Wiener index (B' ; eq. 1) is given in decreasing order for the species in Table VIII. A. chloris exhibits the highest B' , being found at all levels. Five anoles are found in three different perch categories, three at two and one, A. macrolepis, is restricted to a single microhabitat (stream sides and rocks within). The hypothesis that a given species is randomly dispersed among the seven perch microsites is rejected for all but A. chloris and A. biporcatus using the Kolmogorov-Smirnov goodness of fit test (Zar, 1984). A. chloris basically uses most categories of perch microsites, especially in open areas and clearings where other species are absence. Information for A. biporcatus, because of its

TABLE VIII
PERCH MICROSITES

Dispersion of 10 anole species within Bajo Calima among seven microsities. Frequencies of individuals observed, N (relative frequency).

Species	n	Perch microsite (a)					B' (b)	Dmax (c)
		1	2	3	4	5		
<u>chloris</u>	35	4(.11)	9(.26)	13(.37)	8(.23)	1(.03)	.60	5.0
<u>latifrons</u>	21	0(.00)	0(.00)	2(.10)	10(.48)	9(.42)	.40	10.6*
<u>anchicayae</u>	46	0(.00)	0(.00)	23(.50)	20(.43)	3(.07)	.38	18.4*
<u>lyra</u>	22	1(.05)	12(.54)	9(.41)	0(.00)	0(.00)	.36	8.8*
<u>chocorum</u>	10	0(.00)	0(.00)	1(.10)	2(.20)	7(.70)	.34	5.0*
<u>maculivent.</u>	30	1(.05)	21(.70)	8(.27)	0(.00)	0(.00)	.31	12.0*
<u>biporcatus</u>	8	0(.00)	6(.75)	2(.25)	0(.00)	0(.00)	.24	3.2
<u>notopholis</u>	31	28(.90)	3(.10)	0(.00)	0(.00)	0(.00)	.13	21.8*
<u>granuliceps</u>	34	32(.94)	2(.06)	0(.00)	0(.00)	0(.00)	.10	25.2*
<u>macrolepis</u>	18	18(1.0)	0(.00)	0(.00)	0(.00)	0(.00)	.00	14.4*

(a) 1. Ground surface; 2. Bushes, 0 - 2 m; 3. Trunk, 0 - 2 m; 4. trunk and branches 2 - 5 m; 5. Trunk and branches > 5 m.
(b) B' niche breadth (Shannon-Wiener index). (c) Dmax: maximal difference in Kolmogorov-Smirnov goodness of fit test for discrete values, (*) significance at 5 percent.

cryptic behavior and rarity, is insufficient to suggest an actual perch microsite preference. However, it appears to be more common on shrubs.

The dendrogram in Figure 7 graphically illustrates overlap or similarity in perch microsities among anoles. There are two primary groupings, those exploiting the surface (A. notopholis, A. granuliceps and A. macrolepis) and those on vegetation. Within the latter there are three

TABLE IX
NICHE OVERLAP FOR SOME PERCH MICROSITES

Smilarity of 10 anole species as percent overlap calculated following Colwell and Futuyama (1971).

Species	A	B	C	D	E	F	G	H	I	J
A <u>granuliceps</u>	1.0
B <u>macrolepis</u>	.94	1.0
C <u>anchicayea</u>	.00	.00	1.0
D <u>chloris</u>	.17	.11	.63	1.0
E <u>maculiventris</u>	.10	.03	.30	.56	1.0
F <u>latifrons</u>	.00	.00	.60	.35	.10	1.0
G <u>chocorum</u>	.00	.00	.37	.33	.10	.72	1.0	.	.	.
H <u>notopholis</u>	.96	.90	.00	.21	.13	.00	.00	1.0	.	.
I <u>biporcatus</u>	.05	.00	.25	.50	.95	.10	.10	.10	1.0	.
J <u>lyra</u>	.10	.04	.41	.67	.85	.10	.10	.10	.79	1.0

subgroups. The first, composed of A. chocorum and A. latifrons is found in the uppermost trunk, branches and leaves of trees. A. anchicayae and A. chloris, which form the second group, principally exploit tree trunks. The third group, of A. lyra, A. biporcatus and A. maculiventris, usually are found in shrubs. Table IX contains the percentages overlap among all the anole. The highest overlaps (> 0.9) are among surface-exploiting species, but they are spatially segregated horizontally among macrohabitat. Though A. macrolepis and A. granuliceps are found in similar forest macrohabitats, the former is semiaquatic, exploiting stream banks-rocks and debris within the stream. A. notopholis is found in more-open

macrohabitats. A. maculiventris and A. lyra have high overlap (0.85), but are spatially separated by macrohabitats. Figure 8 is a pictorial summary showing the principal dimensions of macrohabitat and perch microsites along which the 10 species of anoles segregate.

TABLE X
MICROCLIMATE DISPERSION

Frequencies (relative frequencies) of individuals observed on three category of microclimates.

Species	n (a)	Sunny	Partial sunny	Shade	B' (b)	Dmax (c)
<u>lyra</u>	22	6 (.27)	14 (.64)	2 (.09)	.37	5.4
<u>anchicayae</u>	48	2 (.04)	28 (.58)	18 (.38)	.35	14.0*
<u>maculiventris</u>	30	1 (.03)	18 (.60)	11 (.37)	.34	9.0*
<u>chloris</u>	35	24 (.68)	11 (.35)	0 (.00)	.27	12.3*
<u>latifrons</u>	21	0 (.00)	6 (.29)	15 (.71)	.25	8.0*
<u>biporcatus</u>	8	6 (.75)	2 (.25)	0 (.00)	.24	3.4
<u>chocorum</u>	10	8 (.80)	2 (.20)	0 (.00)	.21	4.7*
<u>notopholis</u>	31	27 (.87)	3 (.10)	1 (.03)	.19	16.7*
<u>granuliceps</u>	39	0 (.00)	5 (.13)	34 (.87)	.18	21.0*
<u>macrolepis</u>	18	0 (.00)	0 (.00)	18 (1.0)	.00	12.0*

(a) Total number of lizards observed. (b) B', niche breadth (Shannon-Wiener index; eq. 2). (c) Dmax maximal difference in Kolmogorov-Smirnov goodness of fit test for discrete values; (*) significance at 5 percent.

Microclimatic niche breadth and overlap are presented on Tables X - XI and Figure 9. In terms of three divisions (sunny, partially sunny and shaded), A. lyra, A. anchicayae

Figure 7. Dendrogram of perch microsite similarity among anoles at the Bajo Calima study site.

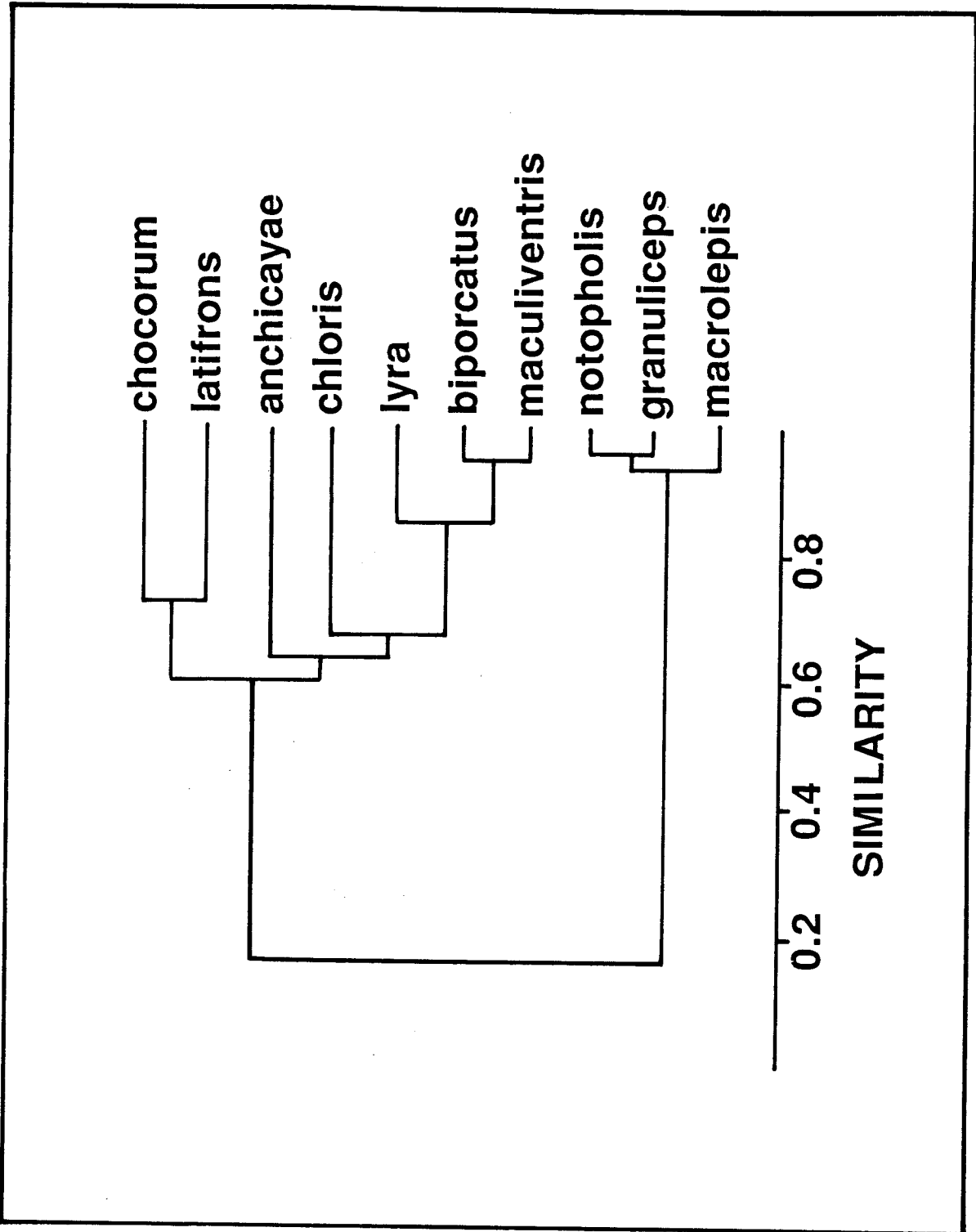


Figure 8. Relation of perch microsities to macrohabitat, vegetational structure and anole body size (maximal snout-vent length).

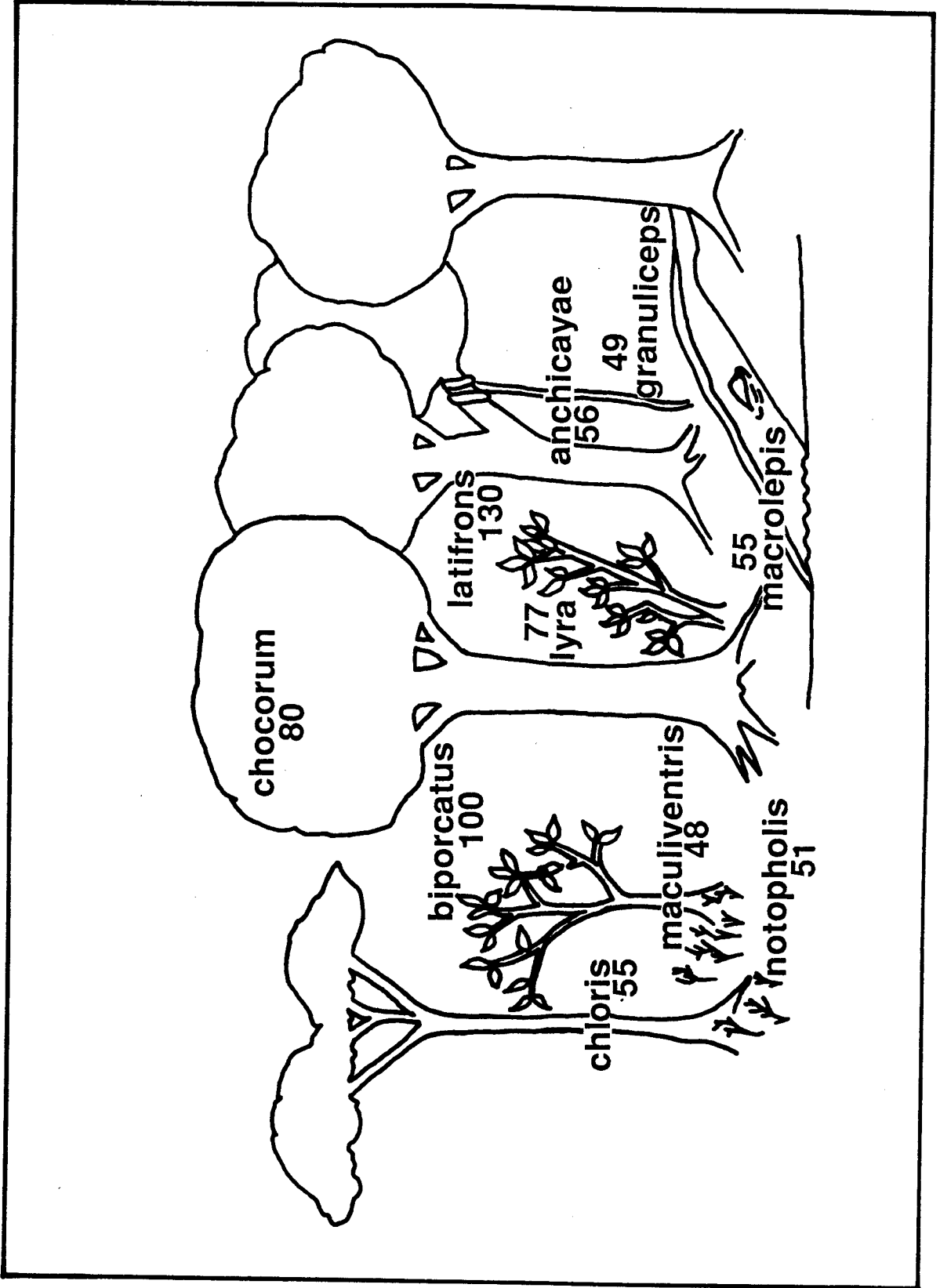
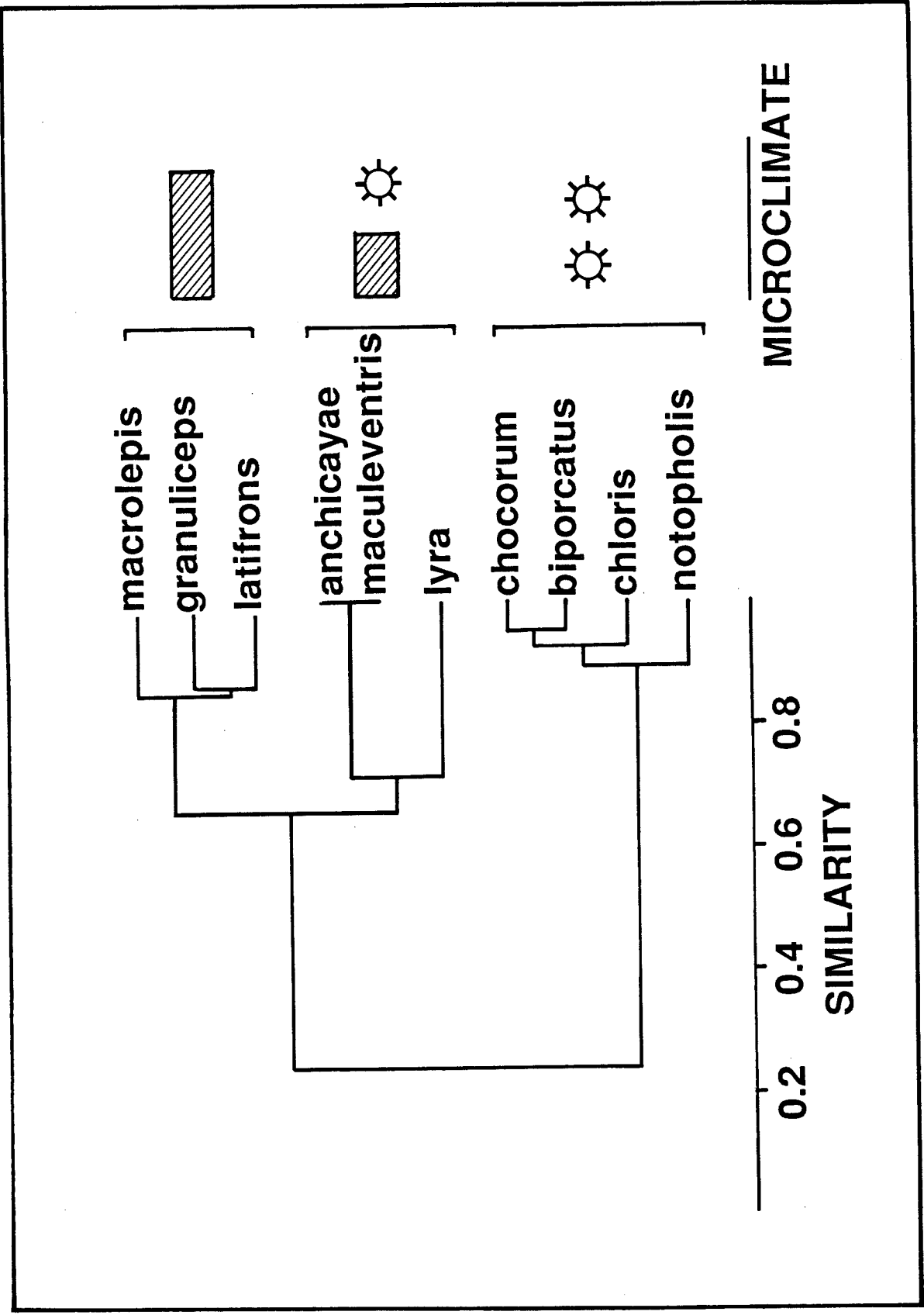


Figure 9. Dendrogram of Perch Microclimate similarity among anoles at The Bajo Calima study site.



and A. maculiventris have the broadest niches, respectively, as measured by B'. Using the Kolmogorov-Smirnov goodness of fit test, the hypothesis that a species is dispersed randomly among the three microclimates is rejected for all but A. lyra and A. biporcatus. A. lyra, an active species, exploits a wide variety of microclimates. As for other niche dimensions, data are too few to describe the microclimatic preference of A. biporcatus. However, since it is found most frequently on bushes it probably exploits sunny microclimates.

TABLE XI

MICROCLIMATIC NICHE OVERLAP

Similarity of 10 anole species as percent overlap calculated following Colwell and Futuyama (1971).

Species	A	B	C	D	E	F	G	H	I	J
A <u>granuliceps</u>	1.0
B <u>macrolepis</u>	.85	1.0
C <u>anchicayae</u>	.52	.37	1.0
D <u>chloris</u>	.14	.00	.35	1.0
E <u>maculiventris</u>	.51	.36	.98	.34	1.0
F <u>latifrons</u>	.86	.71	.66	.28	.65	1.0
G <u>chocorum</u>	.14	.00	.24	.88	.23	.20	1.0	.	.	.
H <u>notopholis</u>	.12	.03	.17	.78	.16	.12	.89	1.0	.	.
I <u>biporcatus</u>	.14	.00	.29	.93	.28	.25	.95	.84	1.0	.
J <u>lyra</u>	.23	.09	.71	.58	.72	.37	.47	.40	.52	1.0

Figure 9 illustrates groupings of the 10 anoles according to their sun-shade preference. Actual overlap or

similarity among species is given in Table XI. Species frequenting shaded patches are principally inner primary forest dwellers (A. macrolepis, A. granuliceps and A. latifrons). As shown in Figure 7, those anoles segregated by perch microsite, A. anchicayae, A. maculiventris and A. lyra, are common to partially sunny areas within their macrohabitat. A. anchicayae has the broadest macrohabitat niche, found in all four principal types. A. lyra and A. maculiventris separate according to macrohabitat (Figure 8). As a group, basking species (A. chocorum, A. biporcatus, A. chloris and A. notopholis) are found in each macrohabitat and at most perch microsites, but individually segregate along those dimensions (Figure 8).

Dietary Dimension

Trophic comparisons among the 10 anoles are given in Tables XII - XIII - XIV and Figure 10. Table XII contains qualitative presence/absence data of the 10 most abundant arthropod prey operational taxonomic units (OTUs; Dunham, 1983) in 181 stomachs analysed for the 10 anoles. Only Hemiptera were absent from stomachs of A. anchicayae, the anole found within all four macrohabitats. A. granuliceps, A. macrolepis, A. maculiventris and A. chloris were found to consume eight different OTUs. Seven OTUs were found in A. notopholis, A. latifrons and A. lyra. A. biporcatus

A. chocorum showed the least diversity in prey OTUs, six and five respectively.

TABLE XII
PREY OPERATIONAL TAXONOMIC UNITS OTUS

Prey operational taxonomic units (OTU) found in stomachs of 10 anoles species from Bajo Calima and similar areas in the Choco.

Species	OTUs (a)										total
	1	2	3	4	5	6	7	8	9	10	
<u>granuliceps</u>	x	x	x	x	x	x	x	x			8
<u>macrolepis</u>	x	x	x	x	x	x		x		x	8
<u>anchicayae</u>	x	x	x	x		x	x	x	x	x	9
<u>maculiventris</u>	x	x	x		x		x	x	x	x	8
<u>chloris</u>	x	x	x	x		x	x	x	x		8
<u>notopholis</u>	x	x	x	x		x	x	x			7
<u>latifrons</u>	x	x	x	x		x	x	x			7
<u>biporcatus</u>	x	x		x		x	x	x			6
<u>chocorum</u>	x	x		x	x		x				5
<u>lyra</u>	x	x		x		x	x	x	x		7
total	10	10	7	9	4	8	9	9	4	3	

- | | | |
|-------------------|----------------|---------------|
| (a) 1. Orthoptera | 5. Hemiptera | 8. Aracneida |
| 2. Coleoptera | 6. Lepidoptera | 9. Diplopoda |
| 3. Diptera | 7. Homoptera | 10. Crustacea |
| 4. Hymenoptera | | |

Prey consumed by all anoles were Orthoptera and Coleoptera. Hymenoptera, Homoptera and Aracneida were found in diets of nine anoles. Lepidoptera, Diptera, Hemiptera, Diplopoda and Crustacea occurred in diets of eight, seven, four, four and three anoles, respectively.

TABLE XIII

DIETS OF 10 ANOLE SPECIES FROM BAJO CALIMA

Relative frequency of prey OTUs in similar areas of the Choco.

Spp. (a)	n (b)	N (c)	OTUs (d)										B' (e)
			1	2	3	4	5	6	7	8	9	10	
A	17	41	.07	.20	.15	.15	.00	.05	.17	.17	.02	.02	.87
B	13	29	.14	.21	.00	.17	.00	.10	.14	.14	.07	.03	.86
C	21	45	.09	.18	.11	.22	.00	.07	.16	.16	.02	.00	.85
D	39	76	.16	.20	.12	.08	.04	.10	.04	.25	.00	.00	.84
E	23	41	.12	.29	.05	.20	.00	.05	.05	.17	.05	.02	.83
F	23	69	.07	.19	.16	.19	.04	.07	.00	.25	.00	.03	.82
G	11	29	.17	.24	.03	.14	.00	.10	.10	.21	.00	.00	.76
H	4	6	.00	.17	.00	.50	.17	.17	.00	.00	.00	.00	.76
I	27	53	.09	.23	.02	.11	.00	.08	.25	.23	.00	.00	.75
J	3	8	.25	.13	.00	.25	.00	.13	.13	.13	.00	.00	.54

(a) Species: A=anchicayae, B=lyra, C=chloris, D=granuliceps, E=maculiventris, F=macrolepis, G=latifrons, H=chocorum, I=notopholis, and J=biporcatus. (b) n= number of stomachs. (c) N=Total number of stomachs containing different prey OTUs. (d) OTU codes same as Table XII. (e) dietary niche breadth (Shannon-Wiener index).

Table XIII shows the dietary niche breadth in decreasing order for the 10 anoles based on 10 prey OTUs, using the Shannon-Wiener index (B'; eq. 2). A. anchicayae, the anole with the broadest macrohabitat niche, has the highest B'. Based only on 10 prey OTUs, most of the anoles show relatively wide dietary niche breadth. A. biporcatus and A. chocorum sample sizes are too small for meaningful inclusion. The former is extremely rare and A. chocorum is

difficult to capture because its high canopy microsite. Figure 10 graphically demonstrates similarity among the anoles, showing relatively little clustering. Again, A. biporcatus and A. chocorum separate out somewhat, but that is because of their small sample size. Table XIV contains the percent overlaps (Colwell and Futuyama, 1971; eq. 4), which are high for the eight species represented by adequate

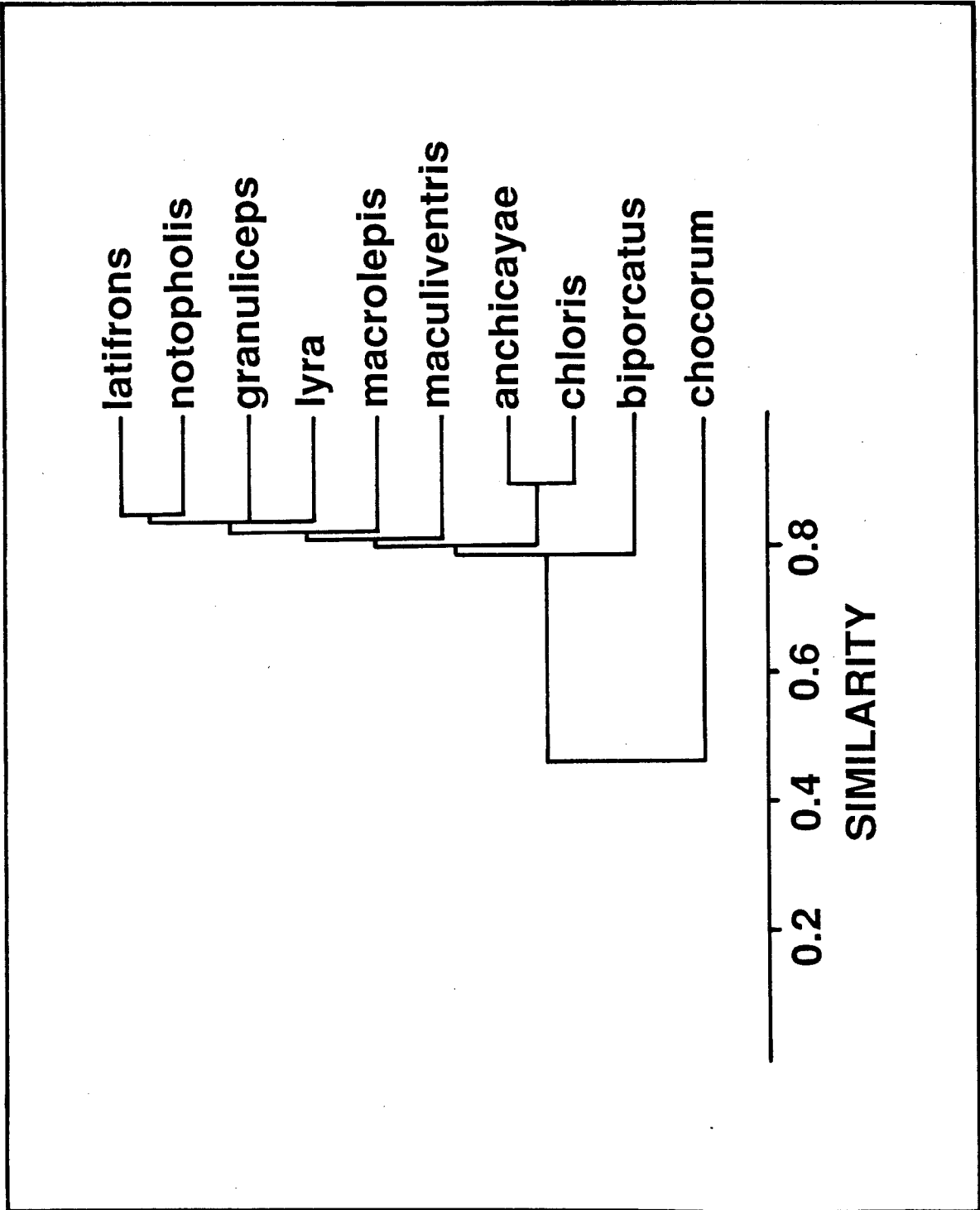
TABLE XIV
DIETARY OVERLAP

Similarity of 10 anoles species as percent overlap calculated following Colwell and Futuyama (1971).

Species	A	B	C	D	E	F	G	H	I	J
A <u>granuliceps</u>	1.0
B <u>macrolepis</u>	.82	1.0
C <u>anchicayae</u>	.74	.80	1.0
D <u>chloris</u>	.73	.77	.89	1.0
E <u>maculiventris</u>	.72	.74	.78	.79	1.0
F <u>latifrons</u>	.83	.71	.76	.77	.80	1.0
G <u>chocorum</u>	.39	.47	.36	.46	.41	.41	1.0	.	.	.
H <u>notopholis</u>	.74	.69	.79	.78	.72	.84	.36	1.0	.	.
I <u>biporcatus</u>	.65	.58	.64	.75	.67	.77	.42	.66	1.0	.
J <u>lyra</u>	.71	.67	.79	.80	.81	.83	.44	.77	.70	1.0

samples. The highest similarity (0.89) is between A. anchicayae and A. chloris. However, they separate among macrohabitats (Table VI; 0.3 overlap) and slightly by perch microsite (Table IX; 0.63 overlap). The second highest similarity (0.84) occurs between A. notopholis and

Figure 10. Dendrogram of diet similarity among anoles at the Bajo Calima study site.



A. latifrons, but they segregate both by macrohabitat (Table VI; 0.3 overlap) and perch preference (Figure IX; 0.0 overlap).

Table XV displays all the prey OTUs (N=17) found in the 181 stomachs according to actual volume and percent volume for each anole. Volume diversity (VD) and OTU diversity (B') are calculated for each anole using equation 2. Those data all summarized in Table XVI, according to decreasing VD'. A. anchicayae, which has the broadest macrohabitat niche, shows both the highest VD and OTU diversities. A. chloris, which has 0.81, is the second in both diversities. Evenness or equitability (E; Dunham, 1983) as calculated by equation 3 is 0.90. Table XVII contains data relating prey size to SVL and general foraging behavior. There is no significant relation between mean snout-vent length and mean OTU volume ($r=0.52$; $0.05 < p < 0.1$) among the 10 anoles. However, as a group larger anoles (mean SVL > 60 mm) consume significantly larger prey OTU (Independent t-test; $t=3.295$, $0.01 < p < 0.02$) than smaller ones (mean SVL < 60 mm). Larger anoles also consume a wider volume range of prey OTUs, having the ability to take larger items than smaller anoles. With the exception of A. macrolepis and A. maculiventris, larger anoles exhibit the highest coefficient of variation (Table XVII) for OTU volumes. A. lyra, the smallest of the larger anoles, has the widest range of prey volumes. Independent

TABLE XV
DIETS ACCORDING TO OTU AND VOLUME

Diets of 10 anole species at Bajo Calima and similar areas of the Choco.

Species	OTUs (a)	Vol (b)	p (c)	f (d)	p' (e)	VD' (f)	B' (g)
<u>A. anchicayae</u>	Orthoptera	85.95	0.12	3	0.04		
"	Homoptera	144.65	0.20	9	0.13		
"	Dermaptera	3.14	0.00	1	0.01		
"	Coleoptera	173.50	0.24	16	0.23		
"	Diptera	78.15	0.11	7	0.10		
"	Lepidoptera	22.28	0.03	2	0.03		
"	Psocoptera	3.35	0.01	1	0.01		
"	Hymenoptera	127.61	0.18	19	0.27		
"	Diplopoda	.19	0.00	1	0.01		
"	Chilopoda	10.47	0.01	1	0.01		
"	Aracneida	68.92	0.10	8	0.12		
"	Crustacea	6.81	0.01	2	0.03		
Total n=17	12	725.02	1.00	70	1.00	.84	.87
<u>A. biporcatus</u>	Orthoptera	20.65	0.05	3	0.23		
"	Homoptera	18.66	0.04	2	0.15		
"	Coleoptera	22.16	0.05	1	0.08		
"	Lepidoptera	242.41	0.52	2	0.15		
"	Hymenoptera	147.77	0.32	5	0.39		
"	Aracneida	14.66	0.03	1	0.08		
Total n=3	6	466.30	1.00	13	1.00	.53	.76
<u>A. chloris</u>	Orthoptera	68.38	0.13	5	0.07		
"	Homoptera	119.92	0.23	12	0.17		
"	Coleoptera	59.45	0.11	15	0.21		
"	Lepidoptera	53.42	0.10	3	0.01		
"	Hymenoptera	129.25	0.25	16	0.23		
"	Diptera	102.02	0.19	11	0.16		
"	Diplopoda	0.14	0.00	1	0.01		
"	Aracneida	33.15	0.06	7	0.10		
Total n=21	8	525.43	1.00	70	1.00	.83	.81
<u>A. chocorum</u>	Homoptera	400.85	0.65	2	0.20		
"	Coleoptera	18.56	0.03	1	0.10		
"	Hymenoptera	182.83	0.29	6	0.60		

"	Hemiptera	18.85	0.03	1	0.10		
Total n=4	4	621.10	1.00	10	1.00	.37	.47
<u>A. granuliceps</u>	Orthoptera	212.21	0.24	15	0.14		
"	Coleoptera	72.83	0.08	19	0.18		
"	Diptera	62.68	0.07	11	0.11		
"	Hymenoptera	45.19	0.05	8	0.08		
"	Hemiptera	60.82	0.07	9	0.09		
"	Lepidoptera	244.92	0.28	11	0.11		
"	Homoptera	11.18	0.01	5	0.05		
"	Colembolla	0.08	0.00	1	0.00		
"	Miriapoda	0.09	0.00	1	0.00		
"	Aracneida	164.42	0.19	24	0.23		
Total n=39	10	874.42	1.00	104	1.00	.78	.88
<u>A. latifrons</u>	Orthoptera	1109.21	0.43	5	0.14		
"	Homoptera	91.27	0.04	4	0.11		
"	Coleoptera	469.21	0.18	9	0.26		
"	Lepidoptera	75.40	0.03	1	0.03		
"	Hymenoptera	164.68	0.06	10	0.29		
"	Diptera	3.67	0.00	1	0.03		
"	Aracneida	564.60	0.22	5	0.14		
Total n=11	7	2557.86	1.00	35	1.00	.61	.74
<u>A. lyra</u>	Orthoptera	428.01	0.06	4	0.11		
"	Homoptera	150.37	0.02	5	0.14		
"	Coleoptera	186.37	0.03	8	0.22		
"	Lepidoptera	1072.68	0.16	3	0.08		
"	Hymenoptera	20.75	0.00	6	0.16		
"	Dermaptera	61.58	0.01	1	0.03		
"	Aracneida	551.87	0.08	7	0.19		
"	Diplopoda	4320.74	0.64	3	0.08		
Total n=13	8	6800.73	1.00	37	1.00	.52	.84
<u>A. macrolepis</u>	Orthoptera	548.38	0.44	10	0.08		
"	Coleoptera	124.99	0.10	23	0.19		
"	Hymenoptera	66.71	0.05	24	0.20		
"	Hemiptera	6.19	0.01	3	0.02		
"	Diptera	116.42	0.09	27	0.22		
"	Lepidoptera	62.64	0.05	6	0.05		
"	Odonata	141.37	0.11	1	0.01		
"	Isoptera	8.55	0.01	5	0.04		
"	Aracneida	154.46	0.13	21	0.17		
"	Crustacea	8.87	0.01	3	0.02		
Total n=23	10	1238.58	1.00	123	1.00	.74	.85
<u>A. maculivent.</u>	Orthoptera	74.31	0.12	6	0.10		

"	Homoptera	4.06	0.01	2	0.03		
"	Coleoptera	202.97	0.33	26	0.44		
"	Diptera	2.60	0.00	2	0.03		
"	Lepidoptera	265.99	0.43	2	0.03		
"	Hymenoptera	47.67	0.08	9	0.16		
"	Diplopoda	0.31	0.00	2	0.03		
"	Aracneida	14.86	0.02	8	0.14		
"	Crustacea	0.08	0.00	1	0.02		
Total	n=23	9	612.94	1.00	58	1.00	.57 .73
<u>A. notopholis</u>	Orthoptera	27.75	0.04	5	0.06		
"	Homoptera	180.03	0.23	18	0.22		
"	Coleoptera	105.92	0.13	24	0.30		
"	Lepidoptera	156.10	0.20	5	0.05		
"	Hymenoptera	165.17	0.21	9	0.11		
"	Diptera	59.90	0.08	3	0.04		
"	Aracneida	94.46	0.12	17	0.21		
Total	n=27	7	789.33	1.00	81	1.00	.79 .75

(a). prey orders. (b). OTU volume in cu. mm. (c) Relative frequency by volume (volume of ith OTU/total number). (d) Absolute frequency/occurrence of each OTU. (e) Relative frequency by OTU (absolute number of ith prey/total number). (f) Volume diversity (Shannon-Wiener index). (g) OTU diversity (Shannon-Wiener diversity indices).

t-tests show significant differences only between A.

latifrons, and A. maculiventris, A. chloris, A. anchicayae,

A. macrolepis, A. granuliceps and A. notopholis (t= 2.49 - 2.68; p=0.01).

TABLE XVI

DIETARY SUMMARY BY PREY OTU AND VOLUME

Dietary summary by prey OTU and volume for 10 species at Bajo Calima and similar areas in the Choco.

Species	n (a)	N (b)	OTU# (c)	Total prey Volume (d)	Volume VD'(e)	OTU B'(f)	E= B'/log OTU
<u>anchicayae</u>	17	70	12	725.0	0.84	0.87	0.81
<u>chloris</u>	21	70	8	525.4	0.83	0.81	0.90
<u>notopholis</u>	27	81	7	789.3	0.79	0.75	0.89
<u>granuliceps</u>	39	104	10	874.4	0.78	0.88	0.88
<u>macrolepis</u>	23	123	10	1238.6	0.74	0.74	0.85
<u>latifrons</u>	11	35	7	564.6	0.61	0.57	0.73
<u>maculiventris</u>	23	58	9	612.9	0.57	0.73	0.77
<u>biporcatus</u>	3	13	6	466.3	0.53	0.73	0.94
<u>lyra</u>	13	37	8	6800.7	0.52	0.76	0.84
<u>chocorum</u>	4	10	4	621.1	0.37	0.84	1.40

(a) Number of stomachs. (b) Number of prey OTUs. (c) Number of OTU. (d) Total prey volume. (e) Volume diversity (see text). (f) OTU diversity. The latter two are Shannon-Wiener indices.

TABLE XVII
RELATION OF PREY VOLUME TO SNOUT-VENT LENGTH

Species	SVL		Prey volume (mm ³)					Foraging behavior (a)
	\bar{X}	SD	\bar{X}	SD	Range	C.V.	S.E.	
<u>latifrons</u>	112	13.3	61.3	125.7	0.1- 763.5	205.0	19.6	S&W
<u>biporcatus</u>	80	7.4	32.5	71.7	0.1- 235.8	220.5	22.7	S&W
<u>chocorum</u>	73	2.2	70.6	113.6	0.1- 339.3	160.9	40.2	S&W
<u>lyra</u>	66	6.9	137.3	402.4	0.1-2094.2	293.1	70.1	AS
<u>macrolepis</u>	52	5.6	11.8	31.4	0.1- 188.5	265.3	3.2	PS
<u>anchicayae</u>	51	3.4	9.8	11.9	0.1- 56.5	121.3	1.5	S&W
<u>chloris</u>	48	4.7	8.5	12.2	0.1- 61.6	143.4	1.5	S&W
<u>notopholis</u>	46	2.1	9.8	14.6	0.1- 103.7	149.2	1.7	AS
<u>granuliceps</u>	41	3.8	9.5	16.3	0.1- 83.8	171.6	1.7	AS
<u>maculiventris</u>	41	3.0	11.3	28.9	0.1- 209.4	256.4	3.7	PS

(a). Foraging behavior: S&W sit and wait, lizard waits for preys on perch; AS active searcher, lizard moves to find prey; PS passive searcher, lizard waits and locates prey then moves to catch them (personal observations on the field).

Morphometrics

Results of the nine morphological measurements for the 10 anole species are given in Table XVIII and comparisons among SVL on Tables XIX. According to SVL, A. latifrons is the largest anole, followed in order by A. biporcatus, A. chocorum, A. lyra, A. macrolepis, A. anchicayae, A. chloris, A. notopholis, A. maculiventris and A. granuliceps. Results of t-test (Table XVIII) show that significant differences in SVL exist between all anoles except for A. granuliceps and A. maculiventris, A. macrolepis and A. anchicayae, A.

chloris and A. notopholis, and A. chocorum and A. lyra.

Most species differ in all morphological measurements (Table XIX). A. granuliceps, A. maculiventris, A. latifrons and A. notopholis are significantly different in all morphometrics from all other species.

TABLE XVIII

BODY SIZE COMPARISONS

Snout-vent length comparisons of 10 anole species from Bajo Calima and museum specimens. Asterisks denote significant differences (Independent t-test; * = $p < 0.05$).

Species	n (a)	SVL		A	B	C	D	E	F	G	H	I	J
		\bar{X}	SD										
<u>granuliceps</u>	34	41.4	3.8
<u>macrolepis</u>	17	51.9	5.6	*
<u>anchicayae</u>	18	50.8	3.4	*
<u>chloris</u>	28	47.5	4.7	*	*	*
<u>maculivent.</u>	23	41.6	3.8	.	*	*	*
<u>latifrons</u>	12	111.7	13.3	*	*	*	*	*
<u>chocorum</u>	6	68.8	9.8	*	*	*	*	*	*
<u>notopholis</u>	32	45.7	2.1	*	*	*	.	*	*	*	.	.	.
<u>biporcatus</u>	11	89.9	10.5	*	*	*	*	*	*	*	*	.	.
<u>lyra</u>	13	66.0	9.2	*	*	*	*	*	*	.	*	*	.

(a) n=number of lizards measured.

TABLE XIX
MORPHOMETRICS OF 10 ANOLES FROM BAJO CALIMA

Morphometrics (\bar{X} SD; mm) of 10 anole species from Bajo Calima and museum specimens from similar areas of the Choco Region. Numbers in parentheses indicate species which are not significantly different (independent t-Test; at $p=0.05$).

Species	N	SVL		Head			Hind limb length	Foot length	Femur length								
		\bar{X}	SD	Length	depth	width											
1 granuliceps	34	41.4 (5)	3.8 (5)	11.6 (5)	1.1 (3,4)	5.4 (3,4)	0.6 (3,4)	6.6 (5)	5.4 (5)	8.8 (5)	1.0 (4)	38.9 (4)	3.4 (4,5)	15.0 (4,5)	1.8 (3,4)	11.5 (3,4)	1.0
2 macrolepis	17	51.9 (3)	5.6 (3,8)	13.4 (3,8)	1.5 (8)	7.0 (8)	0.8 (8)	8.0 (3,8)	0.8 (3,8)	10.4 (3,8)	1.1 (3,8)	46.8	4.6 (3,7,8)	17.9 (3,7,8)	1.7	14.1	1.5
3 anchicayae	18	50.8 (2)	3.4 (2)	14.3 (2)	1.1 (1,4)	5.6 (1,4)	0.6 (2)	7.2 (2)	0.6 (2)	10.8 (2)	0.8 (2)	43.2 (8)	2.0 (2)	18.6 (2)	1.2 (1,8)	11.9 (1,8)	0.9
4 chloris	28	47.5 (8)	4.7 (8)	12.6 (8)	1.1 (1,3)	5.5 (1,3)	0.6 (1,3)	6.8 (8)	0.7 (8)	9.9 (8)	1.2 (1,5)	38.0 (1,5)	3.6 (1,5)	15.3 (1,5)	1.6 (1,5)	11.0 (1,5)	1.0
5 maculivent.	23	41.0 (1)	3.0 (1)	11.4 (1)	0.7 (1)	4.8 (1)	0.3 (1)	5.9 (1)	0.5 (1)	8.8 (1)	0.6 (1)	36.3 (4)	3.2 (1,4)	14.3 (1,4)	1.5 (4)	10.7 (4)	1.0
6 latifrons	12	111.7 (1)	13.3 (1)	30.0 (1)	3.5 (1)	15.6 (1)	2.3 (1)	18.2 (1)	3.8 (1)	23.6 (1)	3.8 (1)	106.7 (1)	11.5 (1)	43.5 (1)	5.2 (1)	30.2 (1)	2.8

7	chocorum	6	68.8 (10)	9.8 (10)	18.6 (10)	3.2 (10)	9.2 (10)	1.6 (10)	10.7 (10)	1.7 (10,9)	14.4 (10,9)	2.4	58.0 (10,9)	41.0 (8,10,3)	22.0 (10,9)	5.6 (10,9)	17.3 (10,9)	2.7
8	notopholis	32	45.7 (4)	2.1 (2,4)	12.7 (2,4)	0.5 (2)	6.6 (2)	0.9 (2)	7.5 (2,4)	0.9 (2,4)	9.8 (2,4)	0.7	43.3 (3)	2.5 (2,7)	17.7 (2,7)	1.4 (3)	12.3 (3)	1.0
9	biporcatus	11	89.9 (7)	9.2 (7)	21.6 (7)	1.6 (7)	12.8 (7)	1.4 (7)	13.5 (7)	1.3 (7)	17.0 (7)	3.0	64.0 (7,10)	9.2 (10)	27.7 (10)	4.9 (7,10)	17.0 (7,10)	2.9
10	lyra	13	66.0 (7)	6.9 (7)	18.2 (7)	1.8 (7)	8.6 (7)	0.7 (7)	11.2 (7)	1.0 (7)	13.8 (7)	1.3	61.0 (7,9)	6.9 (9)	24.7 (9)	2.0 (7,9)	17.5 (7,9)	2.3

CHAPTER VI

DISCUSSION

This study produces the first quantitative data on an anole community within the Choco region of western Colombia. It provides a preliminary description of the diversity and resource partitioning of 10 species of sympatric anoles at Bajo Calima, where exist the most diverse primary forests in the Choco (Gentry, 1986). Central to understanding community structure, within prevailing competitive theories, are accurate descriptions of the distribution and abundance of resident species among/along primary niche dimensions. For anoles studied extensively throughout the Caribbean, sympatric species segregate structurally among macrohabitats and within, among perch microsites and/or prey sizes taken (Rand, 1964; Roughgarden, et al., 1983; Schoener, 1968; Schoener and Gorman, 1968; Williams, 1983). Since anoles in the Caribbean are largely arboreal and prey on arthropods, clear ecological separation (i.e., structural resource partitioning) is expected among sympatric species (Rand, 1964). Field observation by Rand (1964) in Puerto Rico suggest that anoles structurally separate principally by perch characteristics: (1) height; (2); diameter and (3) microclimate (i.e., sun - shade). According to Roughgarden

(1986), anoles in Puerto Rico (Rand, 1964, 1967; Williams, 1983) can be divided according to four structural niches (perch microsites): (1) grass anole; (2) trunk-ground anole; (3) trunk anole; and (4) trunk-crown anole.

Anoles occupying the four perch microsites also show behavioral and morphological differences which are independent of geographical location in the Caribbean. In particular, body sizes of anoles exploiting adjacent structural niche microsites are markedly different; grass anoles are small, trunk-ground anoles are medium-size, trunk anoles are small, trunk-crown anoles are medium size, and crown anoles are large. Williams (1983) calls those similar morphs which occupy similar structural niche microsites ecomorphs. In the Greater Antilles, several species may occupy or exploit similar microsites. However, except for narrow overlap (≤ 1 km; Roughgarden, 1986) species with identical microsite preference are allopatric; no two species with the same niche microsite coexist.

The basic significance of spatial segregation among sympatric Caribbean anoles is conjectural. Two "hypotheses" have been suggested (Rand, 1964) for spatial or microsite separation: (1) it exposes species to different prey, thereby reducing competition for food; and (2) it allows for greater specialization and resource utilization. Those anoles that occupy similar structural niches should separate

more directly in diet (Schoener, 1968). According to Schoener and Gorman (1968), food is partitioned mainly by prey size. Sympatric anoles using the same microsite take different sizes of arthropods (Schoener and Gorman, 1968; Roughgarden, 1983). Roughgarden (1986) reports that anoles on St. Eustatios which show the same microsite preference actually select different prey sizes from those microsites, not from foraging in different microhabitats. In general, there is a relation between lizard body size and prey size taken (Schoener and Gorman, 1968; Roughgarden, 1974).

Results of my study, though preliminary for directly testing theory of island vs mainland diversity, show that anoles segregate structurally along macrohabitat and microhabitat dimensions, including sun-shade preference in ways similar to Caribbean Island species. Based on coefficients of similarity (Whittaker, 1970; Figure 5), the anole fauna at Bajo Calima segregate into forest species and those preferring edges and/or clearings. Vegetational structure appears to play an important role in anole species diversity and anole species diversity (measured as number of species).

Macrohabitat (cultivated zones, open forest, secondary forest and primary forest) is the primary horizontal dimension of the structural niche along which Bajo Calima anoles segregate. Within these habitats seven species are

essentially arboreal, two terrestrial and one semiaquatic. Arboreal anoles are A. latifrons, A. chocorum, A. anchicayae, A. chloris, A. biporcatus, A. maculiventris and A. lyra. A. granuliceps and A. notopholis are terrestrial, with A. macrolepis exploiting streams. As with Caribbean anoles, those at Bajo Calima can be divided by microsite as (1) grass or terrestrial anoles (A. granuliceps and A. notopholis), (2) trunk-ground anoles (A. lyra, and A. maculiventris), (3) trunk anole (A. anchicayae and A. chloris) and (4) trunk-crown anole (A. latifrons, A. chocorum and A. biporcatus). Furthermore, according to microclimate preference they can be divided as basking anoles (A. chocorum, A. biporcatus, A. chloris, and A. notopholis), those which prefer shaded areas (A. granuliceps, A. latifrons and A. macrolepis), and those intermediate (A. lyra and A. maculiventris).

Anoles at Bajo Calima also exhibit a similar general body size-microsite pattern as those in the Caribbean. Terrestrial and trunk species are small, trunk-ground anoles are medium-size and trunk-crown and leaf species are largest. Additionally, anoles at Bajo Calima exploiting branches and trunks where vegetation is most dense (A. chocorum, A. biporcatus, A. chloris, A. anchicayae and A. latifrons) are greener in color than trunk-ground (A. lyra and A. macrolepis) and ground-dwellers (A. notopholis, A. granuliceps and A. macrolepis). See Plates VIII - XII.

The primary forest is undisturbed with complete canopy and some understory, and represents the climax vegetation at Bajo Calima. Anole diversity, however, is less than in the secondary forest ($s=6$ vs $s=10$) where all microsite habitats are found. However, number of species is but a single component of species diversity. The second component is evenness or relative abundance. Since abundance was not determined in an unbiased comparative way the number of species may not be the best indicator. In primary forest there are four principal species. Three in the other two forest macrohabitats and two in the cultivated areas. Species occupying the most disturbed areas, open forests and cultivated zones, (A. notopholis, A. chloris, A. maculiventris and A. biporcatus), originally occurred at the edges and open sites produced by natural events (e.g., storms) within primary forests. Anthropogenic disturbances have enabled them to expand their distributions becoming dominant in open forests and cultivated areas. Continued habitat alteration probably will result in decline of forest species at the favor of A. chloris and A. notopholis, in particular.

In undisturbed primary forests, A. latifrons, A. macrolepis and A. granuliceps are key species. A. macrolepis is confined to shaded streams, exploiting banks, and rocks and debris within their channels. In open more

lighted areas, it is replaced by another Iguanidae Basiliscus galeritus which is ca. five times larger. Juvenile B. galeritus closely resemble A. macrolepis in form and color pattern, suggesting convergent response to exploiting the semiaquatic stream microsite at Bajo Calima. A. granuliceps exploits leaf litter in the shaded forested areas. It is smaller than than the medium-sized A. macrolepis and probably never interacts competitively with it.

A. lyra, a ground-shrub species, may overlap with A. granuliceps though I never observed it to do so. Even so, the former is large and should segregate by diet. A. chocorum is basically segregated from other forest species, occupying the upper canopy. It may overlap in microsite with A. latifrons, but they differ significantly in size. A. latifrons is the largest anole at Bajo Calima, it frequents large trunks of the inner forest. A. chocorum overlaps most with another iguanid, the larger Polychrus gutturosus.

The secondary forest, undergoing succession, is somewhat more structurally diverse. It contains considerable canopy and more understory. There are open areas with increased sunlight and diversity of shrubs among the trees which were not removed during logging. The anole community is most diverse, perhaps because of the greater structural heterogeneity and vegetational diversity in secondary

forests. A. macrolepis, which does not exploit sunlit stream areas is virtually "replaced" by Basiliscus galeritus. A. maculiventris, A. notopholis, A. chloris and A. biporcatus are added to the anole community, with A. maculiventris in greatest frequency. Essentially, the secondary forest contains elements of both primary and open forests, consequently allowing for coexistence of both forest and open area anoles. However, the secondary forest is dominated by A. lyra, A. chocorum and A. anchicayae, which are forest species. A. chocorum is easier to observe in the secondary forest, leading to more frequent observations (Table V). The more open-area species found in the secondary forest (A. chloris, A. maculiventris, A. notopholis and A. biporcatus) are relatively more scarce than they are in open forests because of the more advanced stage of succession.

Open forest exhibits the most disturbance of trees in forest areas. The canopy is non-existent, trees are small and widely scattered. Shrubs, often quite high (ca. 3 m), dominate the open forest. Loss of canopy, its understory and associated trunks combine with greatly increased sunlight to exclude A. granuliceps, A. lyra, A. latifrons and A. granuliceps, the forest species. A. chloris and A. maculiventris become dominant. They are open-areas anoles which favor sunny sites.

Cultivated areas are currently maintained by human activities. They are dominated by grasses and herbs in areas not yet planted with "yuca", banana and "papa china". Trees are principally cultivars, either experimentally planted by foresters or for commercial use (e.g., African palm for oil). As with open forests, which are no longer maintained, there is no canopy. Arboreal perches are virtually non-existent and relatively few shaded areas exist. The only remnants of forest habitats are restricted to stream sides and occasionally found as very small patches among the cultivated zones. The almost complete loss of natural vegetational structure has resulted in the displacement of all forest species, except A. anchicayae, by the open-area species A. chloris and A. maculiventris.

Species diversity of anoles at Bajo Calima appears to be associated with vegetational structural heterogeneity. The more structurally diverse, though human-impacted, habitats possess more perch microsites with attendant microclimates which allow for greater segregation and diversity of sympatric anoles. As arboreal microsites decrease through anthropogenic activities, or natural events such as storms, the diversity of anoles declines.

At Bajo Calima anoles appear more dependent on or limited by availability of microsites than by food resources. At Bajo Calima, anoles have broad diets with high

overlap. Major diet segregation is asymmetrical between large and small anoles. While large anoles can take both small and large prey, small ones are restricted to small arthropods. At present, the abundant arthropod prey at Bajo Calima does not appear limiting because the anoles are clearly segregated spatially and probably do not compete for food. Anoles in the less structurally diverse habitats of the Caribbean Islands probably overlap more spatially and segregate more by diet than those at Bajo Calima. This segregation may cause Caribbean anoles to be food limited (Roughgarden, 1986). Anthropogenic alteration of the natural habitat at Bajo Calima may lead to food limitation and increased interspecific competition, ultimately reducing diversity of anoles.

Summary

The 10 species of anoles at Bajo Calima separate into two principal macrohabitat groups: (1) forest species (A. latifrons, A. chocorum, A. macrolepis, A. granuliceps, A. anchicayae and A. lyra), and (2) those inhabiting openings and edges (A. maculiventris, A. chloris, A. biporcatus and A. notopholis).

The 10 anoles further separate according to ground and vegetation dwellers: A. granuliceps, A. notopholis and A. macrolepis (the latter being a semiaquatic species), and A. latifrons, A. chocorum, A. anchicayae, A. biporcatus, A. chloris, A. lyra and A. maculiventris, respectively.

There is a relation at Bajo Calima between the number of anole species and vegetational structural diversity.

Anole diversity within a given macrohabitat is by perch microsite/microclimate heterogeneity. These are the two major ecological dimensions along which similarity is limited or resources are partitioned.

Pattern of anole body size and perch microsite preference at Bajo Calima is similar to that on the Greater Antilles.

Except in disturbed cultivated areas, no two anoles having similar body sizes share the same perch microsite within a macrohabitat. In cultivated areas the two more opportunistic species A. chloris and A. anchicayae overlap in microsite, but segregate slightly in size and microclimate preference.

No taxonomic prey preference is indicated among the most common arthropods in the anoles' diets. However, prey size range differs among anoles and is related with anole snout-vent length.

Interspecific competition among anoles at Bajo Calima for prey, if it occurs, should be asymmetrical.

Current interspecific competition at Bajo Calima is not evident because of macrohabitat and perch microsite/microclimate structural segregation, and/or body size-prey size preference.

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