Abundance Studies on the Anolis Lizards and Insect Populations of Altitudinally Different Tropical Forest Habitats

Alberto Garcia Moll
Terrestrial Ecology Division, October 1978
Center for Energy and Environment Research Operated by The University of Puerto Rico for the Energy Research and Development Administration

Abstract

The relative abundance of Anolis lizards at four forest habitats selected along an altitudinal gradient in the watershed of Rio Espiritu Santo was assessed by means of daily counts of the individuals. In addition to the parameter of lizard abundance, other correlated parameters were studied such as food abundance, surface availability, number of trees, and number of microclimates at each forest site.

The results indicated an increase in the relative abundance of lizards from higher to lower elevations with the exception of the relative abundance at the mangrove forest habitat, which was lower than at the Roble Blanco forest site (station 3). At site 4, the density of trees and the value of surface availability were the lowest, but the abundance of food was the greatest of all sites.

Therefore, the greater value of lizard relative abundance at station 4 than at station 2 can be ascribed to the effect of a greater food abundance at the former than at the latter station. Also, the relative density of Anolis lizards was greatest at the mangrove forest site (station 4).

The stomach content analyses showed that the available food was selected by the lizards. The frequency distributions of available food sizes were assessed by sampling food items at each of the four forest habitats.

Acknowledgments

The author is grateful to the many persons who collaborated in this study: Richard Thomas made comments on the work at several stages of completion, Richard G. Clements for providing statistical advice and laboratory facilities, Elvira Cuevas for her help with the study proposal, George C. Gorman and Robin M. Andrews for their preliminary advice and discussion.

Francisco D. Folch Castanier commented on the laboratory and field data. Alejo Estrada Pinto and Juan Martinez identified the plant species at the study sites. Brent Holben provided the El Verde computerized weather data. José A. Colón from the National Oceanic and Atmospheric Administration (NOAA) at the Isla Verde Airport supplied weather data. Thanks are also due to Manuel J. Vélez and Gustavo Candelas for their comments on the final draft.

Additionally, José Colón provided his field equipment. Miguel Canals, Felix Santos, Rafael Mosquera, and Luis Negrón González helped in the selection of the mangrove study site and with river transportation. Josefina del Valle typed the draft report and Inés Rodriguez typed the final report. I sincerely thank Provi Sein for her support, understanding, and help.

RESULTS

- TABLE OF CONTENTS
- Previous Studies on the Ecology of Anolis
- Study Sites
- Location and Floristics
- Spatial Distribution of Trees
- Climate
- Lizards
- Relative Abundance Census
- Spatial Distribution
- Structural Habitat
- Climatic Habitat
- Stomach Contents Analysis
- Body Size
- Food Availability
- Surface Availability
- Index of General Species Diversity
- Number and Area of Microhabitats
- Lizards (Anolis Relative Abundance)
- The Zonation Patterns of Anolis Lizards
- Structural Habitat Selection
- Climatic Habitat: Sun or Shade Selection

- Stomach Contents Analysis
- Food Availability
- Number and Area of Microhabitats
- DISCUSSION
- Ecological Aspects on the Anolis Species of the Four Forest Habitats

LITERATURE CITED

6. 10. LIST OF TABLES AND FIGURES

- List of tree species found in the Sierra Palm forest site (Station 1) where 118 trees were considered for the tree species diversity calculations
- List of tree species found in the Tabonuco forest site (Station 2) where 72 trees were considered for the tree species diversity calculations
- List of tree species found in the Roble Blanco secondary succession.

Forest Site (Station 3) considered 127 trees for the calculation of tree species diversity. The only tree species was found in the Mangrove forest site (Station 4), with a total of 53 individual trees. Some patches of grass were mixed with this tree species. The relative abundance of each sex class in every lizard species was found at different altitudes in the topography of the Rio Espiritu Santo watershed.

Lizard relative density was expressed in terms of Anolis relative abundance per: 1) tree, 2) area of topography, 3) tree surface, and 4) m2 of total available surface (ground and tree). The values are 1 x 1072.

Porch availability at each of the four study sites was expressed in terms of m2 of surface: area of ground - tree basal area = available ground area, plus surface of the tree trunks. The different combinations of perch height and perch diameter utilized by the Anolis species sex/size classes (juveniles, females, and males) at each station.

These combinations are given in percentages of the total of individuals belonging to each one of the species' classes. These totals appear to the left of the sex-class categories.

The microclimates of the Anolis species found at the four forest habitats were shown in percentages. The numbers in parenthesis are the total observations for each species at the given site.

Table Page 11, Mean sizes in millimeters and percent variations (increase or decrease) of lizard sex classes from a high to a low elevation. The lowest elevation showed the largest animals of all the sites studied.

12. The diversity of the Anolis and tree species found at the four forest habitats.

13. The estimated cover area of the potentially available microhabitats at the four forest habitats. A. The structural microhabitat cover in square meters; B. The microclimate cover in square meters. The

The ground area of each study site is 450 m2.

Figure Page 1. The general area of the study is located in the northwestern region of the Equisetite Mountains. This map was adapted from a 1976 V. map.

Figure Page 6, Figure 2. An elevation profile ranging from the mouth of Rio Espiritu in the El Verde Area to 884m near Mt. Britton.

Figure Page 7, Figures 3-6. The spatial distribution of large and small trees (see text) found at stations 1-4, respectively.

Figure Page 20, Figure 7. The Anolis relative abundance observed from the highland habitat (1) and along the altitudinal cline to the lowland habitat (4) in the Rio Espiritu Santo watershed. The elevation curve shows the X's and the relative abundance curve shows the O's.

Figure Page 20, Figure 8. The Anolis relative abundances of each of the species found at each of the four habitats. The difference in relative abundance from one station to the next is shown by the segments. See the legend at the right corner for species' symbols.

Figure Page 33, Figure 9. The Lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D).

Figure Page 33, Figure 10. The percent of observations of the Anolis perch height distributions at each forest habitat. The percentage is of total for each sex class/species over the range of perches. The symbols j, f, m indicate juveniles, females, and males, respectively.

Figure Page 44, Figure 11. The percent of observations of each Anolis species at every study site showing the utilized perch diameters.

Table Page 44, Table 11. Mean sizes in millimeters and percent variations (increase or decrease) of lizard sex classes from a high to a low elevation. The lowest elevation showed the largest animals of all sites studied.

Table Page 55, Table 12. The diversity of the Anolis and tree species found at the four forest habitats.

Table Page 55, Table 15. The estimated cover area of the potentially available microhabitats at the four forest habitats. A. The structural microhabitat cover in square meters; B. The microclimate cover in square meters.

Please note, the ground area of each study site is 450 m2.

The study was carried out in the northwestern region of the Luguitio Mountains. This map was adapted from a U.S.G.S map from 1976. It shows an elevation profile ranging from the mouth of the Rio Espiritu, up to the El Verde Area, and reaching 884 meters near Mt. Britton. The spatial distribution of both large and small trees found at stations 1-4 are also depicted (see text for details).

Figure 7 shows the relative abundance of Anolis observed from the highland habitat (1) to the lowland habitat (4) in the Rio Espiritu Santo watershed. The elevation curve is represented by X's, while the relative abundance curve is shown with O's.

Figure 8 demonstrates the relative abundances of each Anolis species found at each of the four habitats. The segments illustrate the difference in relative abundance from one station to the next. The species' symbols can be found in the legend at the right corner.

Figure 9 represents the lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D).

Figure 10 indicates the percent of observations of the Anolis perch height distributions at each forest habitat. Each symbol represents juveniles, females, and males, respectively.

Figure 11 presents the percent of observations of each Anolis species at every study site, showing the utilized perch diameters.

Figure 16 shows the percent relative frequency distribution of the prey lengths found in the stomach contents of all the Anolis lizards captured. The distributions at station 1, 2, 3, and 4 are respectively represented by A, B, C, and D.

Figure 19 illustrates the mean of prey lengths eaten by all individuals sampled at each of the four study sites. The standard error of the means is shown by the rectangles, and the ranges by the bars.

The means of prey lengths eaten by the different sizes of lizards sampled at each study site is also given. The rectangles indicate the standard error of the means, and the bars represent the ranges.

Ranges. Regression lines of the prey length means are shown for each of the stations. Please refer to Table 10 for the sample size of each lizard snout-vent length category.

1. The percent relative frequency distributions of the potential prey lengths sampled at the four study sites.
2. The means of food lengths sampled at each of the four study sites. The standard error of the means is represented by the rectangles, while the ranges are denoted by the bars.
3. The cumulative frequency distributions of the potential prey lengths sampled at the four study sites.
4. The cumulative volume distributions of the potential prey lengths sampled at the four study sites.

The climatic data is averaged for the temperature and rainfall recorded during the period from November to February of the three previous consecutive years; from November 1974 to February 1977.

Introduction

The species composition of Anolis lizards along an altitudinal gradient and the abundance of the geographically embodied species are in part a function of particular physiographic and climatic barriers, modes of dispersal (i.e., terrestrial and arboreal), and food concentration. The ecological conditions affecting the highland species contrast with the conditions affecting the lowland species.

In addition, microhabitat differences dramatically determine the presence or absence of some lizard species within similar climatic regions (Williams, 1969). Some of these ecological differences include intensity of light, air and surface temperatures, relative humidity, rainfall, relative frequency distribution of food sizes, structural surface availability, types of vegetation structure (i.e., grass, ground, trunk, crown) and tree species diversity.

Several hypotheses concerning lizard relative abundance arise when these differences are considered in relation to the adaptations of the Anolis species living at high, intermediate, and low elevations. The most relevant of these hypotheses is that these species show altitudinal variation in their adaptations.

Relative abundance resulting from the different conditions existing in the environments. From this hypothesis, further questions arise as possibly important aspects relating to the ecology of Anolis Lizards. Is food concentration the most plausible biotic factor determining or regulating lizard relative abundance and reproduction? Does temperature affect lizard and insect reproductive cycles more than rainfall does? What would be the effect of the predators of Anolis on their reproduction or survival?

Considering these questions brings up another hypothesis: that food relative abundance increases as a function of increasing temperature. Would this variation be significant from one elevation to the next? In addition, does total surface availability partly determine the abundance of anoles at a given site? How does lizard abundance vary in relation to the available surface? How is lizard density affected by this parameter of the physical environment? In relation to the prey items available at each site, it is plausible that lizards of different sizes would eat any suitable size of food that they can find. Relatively smaller food sizes may represent a higher energy source compared to larger sizes, which are less frequent. Since the lizards of the genus Anolis constitute the most conspicuous and accessible group of vertebrates in the forests of Puerto Rico, a study of the variation of both lizard and resource abundance is one means of understanding the mechanism involved in the regulation of animal populations. The objective of the present study was to assess the abundance of Anolis in relation to food abundance in four altitudinally different forest habitats. In addition, temperature, rainfall, and total surface availability were suspected to be the environmental parameters of higher relevance to the abundance of the anoline lizards in the eastern forest habitats of Puerto Rico which were studied in the altitudinal gradient. Previous Studies on the Ecology of Anolis A wide variety of studies.

Studies have been conducted on the ecology and morphology of these gems in both tropical and subtropical environments, including mainland and island situations. Stejneger (1904) and Schmidt (1978) described the Anolis species of Puerto Rico in terms of their anatomy, microhabitat, and habitat distributions, as well as their geographical distributions on this island.

In a more recent study, Rand (1964) studied the ecological distribution of the Anolis species of Puerto Rico and defined two terms now utilized by most researchers of this genus. These ecological terms are the structural and climatic habitats of the species, or their microhabitats. Collette (1961) and Ruibal (1961) discussed the ecological distribution of Anolis on Cuba in a similar way, as Rand did later on Puerto Rico, utilizing the above mentioned physical parameters of the habitats.

The structural microhabitat was further subdivided by Rand into perch height and perch diameter as an attempt to quantify the previous qualitative microhabitat descriptions. Schoener and Schoener (1971 a, b) made a keen analysis of the structural and climatic habitat of the lowland Anolis species on Jamaica following Rand's (1964) methodology; Rand (1967) studied specifically the ecology and social organization of Anolis Lineatopus on the same island.

They found that body size was determining the perch height and diameter occupied by the species. Similar studies on the ecological significance of animal size, including intraspecific differences, have been made by Schoener (1967, 1968, 1970), Schoener and Gorman (1968), and Andres (1971). Ruibal and Philibosian (1974) also addressed microhabitat utilization in their population ecology study of Anolis acutus on St. Croix, U.S. Virgin Islands.

Many studies on the anoline lizards of the Caribbean islands have also dealt with the possible history of colonizations as shown by their geographical distributions (Williams, 1969; Gorman and Atkins, 1967, 1969; Gorman, Thomas, and Atkins, 1968; Levins and Heatwole, 1965). Data on the habitats,

Microhabitats, and food habits have been reported for A. conspersus (Schoener, 1967), A. Limifrons (Sexton, Bauman, and Ortleb, 1972), and A. Lineatopus (Rand, 1967). These studies have documented a maximum mm mean prey size eaten by these Molis species, a value not significantly different from the mean food length available at those respective habitats.

Studies on the altitudinal effects of climate on the reproductive cycles of some Puerto Rican Anolis species have suggested that temperature and daylength may cause the initiation and end of egg and sperm biosynthesis (Goman and Licht, 1974; Licht and Gorman; 1975). In winter, daylength is shorter and temperature is cooler, resulting in a reduction of testis size. Fattening may occur without an increase in the food availability of the habitat as a result of the reduced "reproductive effort" of males during this season (Licht and Gorman, 1975). However, with experiments utilizing translocated caged populations, they have shown that the fat reduction occurring during the peak of the breeding season may be due to a limited food energy supply, and that fat increase per se does not cause the decline in testicular activity. Thus, this may imply that lizards have physiological control over the partitioning of food.

Food availability on islands may be small, but relatively higher during the Molis breeding season when temperatures show an average increase, though lizards show a response to these little variations. As more energy is channeled into reproduction, fats cannot be stored as when this activity stops or is reduced. Andrews (1976) studied the growth rates of mainland and island Anolis lizards. She has suggested that the greater growth rates of the mainland over the island species support the hypothesis that "island anoles may be generally food-limited and mainland anoles not so limited."

Studies on food supplementation (Licht 1974) and seasonal effects (Licht and Goman, 1970) have documented growth by fattening in Caribbean adult Anolis, while

Hatchlings of A. Limifrons in Costa Rica (Andrews, 1976) did not grow faster under conditions of high food abundance, suggesting that they may be growing at physiologically maximum rates in the field. Andrews in this study also demonstrated that island anoles may allocate more energy to feeding activities, as did A. Oculatus on Dominica. This species moved more frequently and ate numerous small prey items, suggesting a more active foraging strategy than A. Limifrons, which ate fewer larger food items.

In addition to low food availability, Itch (1972) suggested that the relatively low temperature of the montane cloud-forest habitats in Costa Rica is the growth limiting factor for A. Tropidolepis. The mean annual temperature of the habitat of 17°C is similar to Puerto Rico's Luquillo palm brake and cloud-forest habitat temperatures during the cooler winter months.

Contrary to the widespread misapprehension that seasonal changes do not take place in tropical climates, Dobzhansky and Pavan (1950) found that variations in the relative frequencies of Drosophila flies took place even from month to month in Brazil. They also observed that some portions of a habitat showed higher insect concentrations than other portions and attributed this variation to heterogeneous food source distributions. They reported that some of these habitat portions had a higher concentration of decomposing organic matter, such as fruits and logs, than did others. They suggested that the diverse number of microhabitats was also determining the diversity of species of Drosophila because these different food sources constituted the diversity of fruit trees where the flies selectively fed.

Materials and Methods

Study Sites Locations and Floristics

Four sites were selected for study in the watershed of the Rio Espiritu Santo (Fig. 1) beginning near the headwaters southwest of El Yunque Peak and ending in the estuary east of the town of Rio Grande (Fig. 1).

2). The altitudinal cline was chosen, including two extreme stations and two intermediate closely located ones. The sites are a Sierra palm (Prestoea montana) brake at 850 m, a Tabonuco/Ausubo (Oacryodes excolse/Manilkara bidentata) forest at 410 m, a Roble Blanco (Tabebuia heterophylla) forest at 250 m, and a Mangle Blanco (Lagucularia racemosa) forest at approximately 1 m. Tables 1-4 show the tree species composition, their relative frequencies, and the total number of trees in each of the latter sites. In each of these, 450 m^2 were measured in a 30 m x 15 m plot approximately oriented to the magnetic North. The slope orientation in the three mountainous forest sites is approximately westward. The North and South ends of the plots were 15 m wide each. All trees greater than 2.5 cm DBH (diameter at breast height) were included in the tree censuses. These were given a number in the order of appearance and then mapped (Figs. 3-6).

Climate monthly average rainfall and temperature were obtained from the National Oceanic and Atmospheric Administration (NOAA) and the Center for Energy and Environment Research (CEER). Data from NOAA weather stations in Canovanas (18°24'N, 66°54'W, nominal) at 8.5 m and El Verde, Rio Grande (18°21'N, 65°49'W, nominal) at 60.9 m were used as estimates of temperature and rainfall at the Rio Espiritu Santo Estuary study site, and rainfall at the Roble Blanco site at El Verde, respectively. In the latter site, specifically, air temperature below the canopy was measured by the author. The data from the CEER weather network was recorded for temperature and rainfall.

300: 200: ELEVATION ABOVE SEA LEVEL (M) 100. DISTANCE FROM SHORE (km)
Fig. 2. Elevation profile ranging from the mouth of Rio Espiritu Santo, up El Verde area, to 884 m near Mt. Britton.

Table 1. List of tree species found in the Sierra Palm forest where 118 trees were counted for tree species diversity.

Species Relative Frequency
Prestoea montana 0.64
Celycogoniua

Squamsolean 0.15 Psychotria berteriana 0.08 Eugenia borinquensis 0.03 Cecropia peltata 0.02 Miconia guianensis 0.02 Sophia bryophile 0.01 Ardisia placiflora 0.01 Githarexylum caudatum 0.01 Clusia gundlachii 0.01 Cordia borinquensis 0.01 Micropholis garciniaefolia 0.01 Myrcia splendens 0.01 Tabebuia rigida 0.01

Table 2. List of tree species found in the Tabonuco forest site where 72 trees were considered for the species diversity calculations.

Tree Species Frequency: Manilkara bidentata 0.25, Tetragastris balsamifera 0.03, Teichilia pallida 0.03, Andira inermis 0.01, Alchornea portoricensis 0.01, Cassipourea guianensis 0.01, Guarea racemiflora 0.01

Table 3. List of tree species found in the Roble Blanco secondary succession forest (station 3) where 127 trees were considered for the calculation of tree species diversity.

Tree Species Relative Frequency: Tabebuia heterophylla 0.62, Myrcia splendens 0.09, Psychotria berteriana 0.07, Toga Leurina 0.05, Casearia sylvestris 0.03, Dendropanax morototoni 0.03, Nectandra sintenisii 0.02, Miconia prasina 0.02, Cyathea arborea 0.01, Myrcia deflexa 0.01, Prestoea montana 0.01, Swietenia macrophylla 0.01

Table 4. This was the only tree species found in the studied mangrove forest site. The total number of individual trees was 3. Some patches of grass were found mixed with this tree species.

Tree species Relative Frequency: Avicennia germinans 1.00

Figs. XA), 4B), 4C), 4D). The spatial distribution of the large and small trees found in different sections respectively.

Data were utilized as estimates for the nearby Sierra palm brake and Tabonuco/Ausubo forest sites. These data were available only from January, 1976 to May, 1977, except for the data recorded at the El Verde Field Station, of which, only the period from 1974 to 1977 was utilized. The temperature and rainfall monthly means at each station.

The text corrected:

Including November, December, January, and February, the averages were taken for three consecutive years. The rainfall and temperature patterns observed during the study period in the four habitats might provide insights into the geographical variations in the relative frequencies of some arthropods, mainly insects, and on the primary productivity of forests.

Lizards: The most accessible Anolis species were studied at the four forest habitats included in the altitudinal gradient. Since A. cuvieri and A. occultus are less conspicuous species or occupy less accessible micro-habitats, even though they are expected to occur across and along the more inland parts of the gradient, they were not included in the present work.

Relative Abundance Census: Daily Anolis counts were performed at each station, beginning at the palm break. Each species' sex classes were counted at regularly spaced time intervals. Sex classes will be defined in terms of body length below. Approximately 16 rounds per site were finished in four days. Since the relative abundance method did not include marking lizards, repeated lizard counts were avoided by zigzagging the 450 sq. m. area in a south-north-south fashion along the five 30 m columns. From the data collected at each station, I selected the highest count for each individual sex class belonging to the different species. Then, the total of frequencies were added, and the relative abundance calculated.

I believe this process of calculating relative abundance (by yielding the highest number per day of a species' sex class) to be fair enough in terms of expressing an estimate of the total relative abundance in each site. However, for other purposes (e.g., lizard activity patterns) this way of calculating could alter the proportions among the sex classes of different species on a given day. The relative abundance data have been employed to estimate relative lizard densities in the altitudinal cline according to the total number of trees and various area units following a simple calculation.

The total relative frequency of each site was divided by 1) the total number of trees, 2) square meters of topographic area, 3) square meters of tree trunk surface area, and 4) square meters of total available surface area. The last two area units will be described later under Surface Availability.

Spatial Distribution: One of the various types of data collected when an individual lizard was first spotted was its location on a tree perch. Each day depicts a spatial distribution pattern. For this purpose, an activity period has been selected from each habitat. The criterion used was the degree of activity during the period that could show the structural habitat partitioning on a horizontal level, e.g. zonation, without considering stratification. Thus, the most active period at each site was chosen.

Structural Habitat: The height and diameter of the perches where individual lizards were first seen were recorded using the conventional method used by Rand (1964). These measurements were approximations made by the same person.

Climatic Habitat: Anolis Lizard species have different climatic adaptations. As a result of these adaptations, these species occupy sunny and shady areas, and often intermediate zones. This data was also collected when lizards were first spotted during the relative abundance censuses. In addition, the species' sex classes were identified at the same time. Then, the frequencies of all sex classes found under the three climatic categories were separately added and expressed in relative frequency percentages.

Stomach Contents Analysis: Lizards are typically active throughout the day with a few exceptions. They also become active early in the morning as they warm up to their optimal temperatures or as light allows them to move around their habitats. Presumably, lizards eat sufficient quantities of prey items during the morning hours that one may suspect their stomachs are full or almost full thereafter. Utilizing this criterion, I collected all the...

Lizards were active in the 450 sq. m. area around 1200 hours. The collected animals were immediately euthanized with a small dose of 10% formalin. The peritoneal cavity was then filled with Turtox Insect Preservative to preserve the stomach contents. I refrained from injecting the stomachs directly to prevent disorganizing the prey inside. The stomach contents were analyzed with the use of a binocular microscope. The purpose of the analysis was to determine the prey length frequency distribution at each study site. Taxonomic classification (or quality) of prey items lies beyond the scope of this work. The size of prey eaten by anoles is defined here as the prey length.

Body Size: While in the field, after a lizard had been collected, the snout-vent length was measured from the tip of the snout to the cloaca. Sex classes were defined according to the snout-vent lengths and sexes. Sometimes, different anoline species reach sexual maturity at different body sizes. Also, the members of a species may differ in size from the members of another species. Therefore, the snout-vent length means for the upper class intervals of each species sex classes are presented in Tables 10 and 11 below.

Food Availability: The food available at each site was measured by placing 50 km^2 sticky traps at 1200 hrs. for a 24-hour period. Arthropods, including several orders of insects, were captured on a 2 m-thick tanglefoot layer smeared over the white metal plates. A rough estimate of the volume of food items was calculated by multiplying each size category by its frequency. The total of food censuses was completed in three months: mid-November, December, January, mid-February, at stations 1, 2, 3, and 4, respectively. Starting in late November, censuses were made every three weeks. The purpose of these censuses was to compare altitudinally different sites and not seasonal variations within sites. I assumed the seasonal variation in relative abundance that may have occurred in a period of three months did not exceed the magnitude of the

Altitudinal variation in relative abundance along the cline is evident. Anolis lizards utilize different portions of the habitat according to their morphology and physiology. Therefore, the total available surface area was estimated for each of the four forest habitats. This total includes the site area minus the basal area, which equals the ground surface plus the surface area of tree trunks.

The basal area is the cross-section area of the trunks, approximately the area of a circle. The surface area of tree trunks was roughly estimated by calculating the area of the cylinder (the trunk), using the height and diameter of the tree.

The formula used for the Index of General Species Diversity is Shannon's: H= -E Pj log Pj. Here, Pj represents the importance probability for each species (nj/\), N equals the total number of individuals in the study site, and ni are the individuals belonging to each species (Shannon and Weaver 1963; Margalef, 1968).

The microhabitat of the anoles at ground level was classified as: 1) understory vegetation, and 2) leaf and wood litter. The surface area of trunks was discussed under Surface Availability but is also included here as one of the microhabitats of the lizards. The ground cover areas were estimated in square meters by utilizing the data on ground cover and soils covered by litter in each of the 509 sq. m. (or 3m x 3m) subplots.

The density of the forest canopy and the development of understory vegetation have a cause-and-effect relationship in forest habitats. The denser the canopy, the more limited the understory growth (Lugo, 1970).

The microclimatic habitat of Anolis Lizards is determined by the solar energy entering the forest habitat. Forests will provide either heavy shade, intermediate solar radiation, or sunnier spots depending on their canopy densities. In addition, there will always be spots in constant shade, but in others, some variation in the duration of sunlight may occur as the day progresses.

Result of the Earth's rotation. The following categories were used to report the estimated microclimatic areas available at each of the four forest habitats: 1) Shady, closed canopy - defined by a dense shade microclimate with almost no sunflecks; 2) Intermediate, semi-closed canopy - defined here by opened canopy/closed canopy <1; and 3) Sunny, semi-opened canopy - defined by opened canopy/closed canopy >1. The number of subplots belonging to the microstructural and microclimatic habitats can be assessed by dividing the square meters by 9 sq.m.

Each subplot was observed to be approximately uniformly covered by a specific microstructure (e.g., understory vegetation, litter) and microclimatic category.

Results: The lizard relative abundance data are presented in Figures 7 and 8. Figure 7 shows the total number of individuals per day at each site. An increase was observed from station 1 to 5 and a decrease from 3 to 4, but to a greater relative frequency than in station 2 at 410m. The frequencies at stations 1, 2, 3, and 4 were, respectively, 51, 43, 59 and 49.

The relative abundances of each of the lizard species found at each elevation are presented in Figure 8. Utilizing detailed data, I observed the following relative abundances of each of the sympatric species: at station 1, 26 A. gundlachi and A. evermani; station 2, 19 A. gundlachi, 2 A. evermanni; 2 A. stratulus, and 1 A. cuvieri; and at station 3, 55 A. gundlachi, 9 A. evermanni, 6 A. stratulus, 5 A. krugi, and 5 A. cristatellus.

At station 4, evidently, A. gundlachi, A. evermann, and A. krugi, which are some of the high elevation species, were not found. Anolis evermanni is sometimes found at low elevations, but not in the Rio Espiritu Santo mangrove forest. These three species were replaced by their counterparts at lower elevations: A. cristatellus, A. stratulus, and A. pulchellus. Their respective observed relative abundances were 27, 14, and 8.

In Table 5, appears the relative abundance and percent variation of...

---Page

Figure 7: The number of Anolis individuals observed per day. Relative abundance of Anolis in the highland habitat (1) and along the altitudinal cline to the lowland habitat (4) in the Rio Espiritu Santo watershed. The elevation curve shows the X-axis and the relative abundance curve shows the Y-axis.

Figure 8: The relative abundance of each Anolis species found at the four habitats. The change in relative abundance from one station to the next is shown by the segments. See the legend in the right corner above for species’ symbols.

Table 5: Relative abundance of each sex class in every lizard species found at different altitudes in the topography of the Rio Espiritu Santo watershed. The table shows the variation in relative abundance of lizard size and sex class intervals at different stations.

This table also shows the relative abundance of each species' sex class at different elevations. Generally, the relative abundance of individuals, including adult males and females and juveniles, increased from higher to lower elevations. The discussion will not focus on the observed differences in sex ratios within individual species from elevation to elevation, as this specific issue lies beyond the scope of the present work.

In Table 6, the conversion of the lizard relative abundances into the relative densities, not biomass, of the lizards at each altitude is shown. First, although at station 4, the...

The relative abundance of Anolis was lower (49) at station 3 (59). The lizard's relative density doubled at station 4 since I only counted half the number of trees found at station 3. The difference in the number of trees may be explained on the basis of successional stages. The Roble Blanco lower montane forest (station 3) was a monoculture about 40 years ago and is now in secondary succession, while the Mangle Blanco forest is at a climax habitat in pulse stability (Odum, 1971). Secondly, the total surface availability was significantly greater in the Tabonuco/Ausubo and the Roble Blanco forests than in the Sierra Palm Brake and the White Mangrove forests (Table 7). Nevertheless, lizard relative density increased from the Sierra Palm Brake and the Tabonuco/Ausubo forests (stations 1 and 2 each with 4 x 10° lizards/m2) to the Roble Blanco and White Mangrove forests (stations 5 and 4 with 7 x 10-2 and 8 x 10-2 lizards/m2, respectively). Thirdly, the surface area of the trunks is particularly important to A. gundlachi, A. evermanni, A. stratulus, and A. cristatellus.

Table 1: Perch availability in each of the four study sites expressed in terms of % of surface area of ground vs. tree basal area vs. available ground area vs. surface of tree trunks.

Stations: 1 2 3 4

450.00 = 1.74

450.00 = 2.93

450.00 = 1.55

450.00 = 0.790

Respective totals: 448.26 447.07 448.45 409.21

Plus: 319.95 544.87 452.84 169.27

Equals: 768.21 991.94 901.29 618.48

Table 6: Lizard density expressed in terms of Anolis relative abundance per: 1) tree, 2) m of topographical area, 3) m2 of tree surface, and 4) m of total available surface (ground and tree). Values are x 10°2.

STATIONS: 1 2 3

1: 2 33 94

2: 7 10 3

3: 10 8 3

4: 4 4 7

5: 8 24

During the day, these species primarily utilize trunks. As a result, trunk surface area was correlated with variations in lizard relative densities at the four study sites. Accordingly, lizard relative density increased in sites where trees were shorter and had smaller diameters (at breast height), and where

Lizard relative abundances were greater. Compare the "#" row (surface area of trunks) in Table 7 with the #3 row (relative abundance/number of tree surface area) in Table 6. Thus, the relation between lizard relative abundance and trunk surface area has been considered here of particular importance to anoles and will later be addressed in the discussion.

The Zonation Patterns of Anolis Lizards

The horizontal distribution of the lizards observed during a period of approximately 1.5 hours on a given census day at each of the forest habitats is presented in Figure 9. The patterns of spatial distribution of the lizards at all the sites may be described as groups at random or clumped distributions.

At station 1, the chosen period was 1000-1130 Hrs. on 20 Nov., 1976; at station 2, 1350-1445 Hrs, on 15 Dec., 1976; at station 3, 1515-1450 hrs, on 31 Jan., 1977; and at station 4, 1000-1145 hrs. on 11 Feb., 1977.

The number of anoles per tree during that period at the highland palm brake habitat was mainly one (81% of the 21 lizards) and with two exceptions two lizards per tree (19%). At the next highland intermediate habitat (station 2), where Dacryodes excelsa (Tabonuco), and Manilkara Bidentata (Ausubo) were the dominant tree species, the anoline lizards perching "solitarily" were relatively less grouped together than at the Prestoea montana palm brake. This may be as a result of the greater distances between the larger trees of that habitat which could have

Fig. 9. The Lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D)

determined the closeness of one individual lizard to the other. However, the percentage of anoles at station 2 during the selected high activity period out of 31 lizards was 64% alone on a perch, 26% in individual pairs, and 10% together. In this case, it seems that the occurrence of pairs (at the same time and perch) may be the result of 1) reproductive behavior, 2) the diameter of the perch or

The text should read:

Availability of surface area, and 3) a greater local food availability within the microhabitats. The trees at the SE and W, with 2 and 5 lizards respectively, are evidence for the second alternative. Lower along the altitudinal cline, the relative abundances and densities of Anolis lizards increased moreover. At station 5, I observed that the number of pairs per perch, during the chosen high-activity period, became more frequent than at the above described habitats. Out of 48 lizards, 56% were found alone, 38% were in pairs, and 68 together. Also, the 'solitary perchers' were closer together than at the two above habitats. The section ahead which deals with the available structural and climatic microhabitats may explain why there were that many lizards together. The relevant data indicate that the higher the number of available microhabitats, the higher the number of species and total of individuals that can be present at this habitat. In addition, the relatively high food relative abundance at this intermediate elevation, compared to the high elevation, may be supporting a greater relative abundance of lizards. At station 4, the mangrove forest site, where a greater food supply was observed to be composed of small crustaceans (e.g., fiddler crabs and isopods) and where there was a smaller number of trees, the lizard distribution pattern of the selected period was similar to those of the other three study sites. Nevertheless, in one large tree there were four Anolis cristatellus (out of 59): two females and two males.

This was exceptional and may be explained by the much greater food relative abundance at this site. Most of the lizards perching alone (46%) were observed on the large trees. The pairs (36%) were seen on either clusters (on small trees) or on the grassy areas at the N part of the mangrove forest near the grassland. Also, three lizards (8%) were found at that time period at a cluster. In conclusion, the patterns of on-site distribution did not seem to vary greatly along the

Altitudinal Cline: With the increase in resource availability or with higher anoline relative density, structural habitat selection changes. The table summarizes all the different combinations of perch height and diameter utilized by the sex-classes of the species in the forest habitats. Figures 10 and 11 show the perch heights and perch diameters chosen by the different Anolis species, respectively. On the basis of structural habitat, we can describe the microhabitat of the anoline species at different habitats. Those species found at more than one habitat consistently showed very similar structural habitat selection, although they were not mixed with the same congeners, number of species, nor did they occur at the same abundances.

At stations 1, 2, and 3, Anolis gundlachi juveniles mainly occurred close to the ground and on perches up to 2 meters high of small (1 cm) to moderate (8 cm) size or diameter. A. gundlachi females, at the same stations, were mainly found from 1 to 2 meters above ground on small to large (2 to 16 or more centimeters) perches, and A. gundlachi males primarily at perch heights from 1 to 3 m above ground on perches of moderate to large (8 to 16+ cm) diameters.

Anolis evermanni juveniles were observed more frequently at perch 28.

Figure 10. The percent of observations of the Anolis perch height distributions at each of the forest habitats. Percentages are of total for each sex class/species over range of perches. The symbols j,f,m indicate juveniles, females, and males, respectively.

NUS started on page 56 with an analysis of PERCH DIAMETER (in CENTIMETERS) for each Anolis species. The study showcases the utilized perch diameters and heights of 1 to 3 meters on perch diameters ranging from less than one centimeter to sixteen, at the first three sites where they occurred. All sites were included except for the mangrove forest site.

A. evermanni females were found on high perches ranging from 1 to over 3 meters, and of small to large sizes (2 to more than 16 cm). At the Sierra palm brake (station 1), A. evermanni males were observed only three times at 2 meters and at more than 3 meters on very high palm canopies, and on moderate to large perch sizes.

At station 2, the montane forest, these males occurred lower, closer to the ground and very high at more than 3 meters, on moderate to large diameters of 8 to more than 16 cm. At station 3, A. evermanni males were distributed on perches very similar to those at station 1, where they did not come very close to the ground.

Anolis stratulus juveniles were observed at perch heights of 1 to 2 meters at stations 2 and 3, but at station 4 they climbed higher up to more than 3 meters on the small to moderate (1-8 cm) perches. These juveniles, at sites 2 and 3, were observed on perch diameters of 1 to 8 cm and 2 to 16 cm, respectively.

The females perched primarily at perch heights of 1 to more than 3 meters, and on perches of small to large sizes (1 to more than 16 cm), at stations 2, 3, and 4. The males were found as high as females and on similar perch diameters at stations 3 and 4.

One Anolis cuvieri juvenile was found at station 2 on a 2 cm small perch at 2 meters high. Anolis cristatellus juveniles occurred fairly close to the ground at stations 3 and 4, and up to 2 meters on very small (<1 cm) to moderate (8 cm) perches.

The females were found close to the ground and up to 2 and 3 meters high at stations 3 and 4, respectively. They perched on small to large diameters at station 4, and on moderate to large diameters at station 3. The males, at station 4,

Sometimes, they perched either very high at more than 38m (similar to A. stratulus, A. gundlachi, and A. evermanni males at their respective sites) or fairly close to the ground at less than 1m, similar to A. evermanni males at station 2. Anolis kmugi juveniles, found at station 5, occurred in the understory ground vegetation of the site and climbed up to 1m high on small saplings and seedlings of less than 1cm wide. The females perched higher than the latter and utilized small to moderate (1 to 8 cm) perch diameters. The males perched similarly, but on larger perch diameters than the females. Anolis pulchellus, found at the lowland study site, utilized the ground cover more frequently than its congeners. The juveniles were only found on the ground, the females on the ground and at 2m high, and the males also on the ground and at 5m high. Perch diameters utilized by both, females and males, were very small to moderate sizes.

Climatic Habitat: Sun or Shade Selection

Climatic differences were expected at the different altitudes chosen for this study. These differences will be outlined later under Climate. As a result of these variations, different species were found at the altitudinal extremes and were classified as highland and lowland species. At the intermediate elevations, the highland species were found in the more shaded areas of trunks or ground cover, and the lowland species replaced them in the unshaded and sunnier conditions (Table 9). Anolis gundlachi, which has always been considered by anoline ecologists to be a highland shade-adapted species, was found about 80% under heavy shade. A. evermanni, considered a highland species too, was found 83% in sunny or, at least, sunnier situations at the high elevation (station 1), but at the intermediate elevations was about 66 to 93% in shady areas.

The rest of the text seems to be a mix of incomplete sentences and out-of-context phrases. To provide a more accurate correction, more context is needed.

LEVEL TO WIN10 STONY seems way off and so does type 20; such errors go to 92 and are specialized in an exciting buzz. "Squared in unity, 3033 key 382303, there are 2 games to be played. STTOUY or Jo saw ETTOOISTU ay "g STEEL 37.

Highland species, sun-adapted in a high elevation habitat, have been found in the more shady microclimates at lower or intermediate elevations. A. stratulus, a lowland species, was found in shaded and slightly unshaded microclimates at station 2, since this forest habitat is mainly composed of dense shade and some sunnier microclimates at the forest margins. Microclimate availability at each site is reported below under Microhabitat Availability.

At station 3, the next intermediate elevation, A. stratulus perched under a variety of microclimates. In the lowland, this species shared the sunny microclimates on tree trunks with A. cristatellus in a proportion of 66 to 78%, respectively. A. cristatellus showed less preference for shade than A. stratulus. The number of observations of A. cristatellus at station 3 was too small to be significant for analysis; but nevertheless, this species would be expected in shade 67% of the time and in sun 35%, as the result of their optimum structural habitat being occupied by its morphologically similar congener A. gundlachi. In addition, the latter was a dominant species over the former.

Anolis krugi was found at station 3 occupying mostly those shaded areas near the ground. This was also expected for a highland species found at intermediate altitudes. Anolis pulchellus occurred 85% in sunny situations and 15% in unshaded cooler microclimatic habitats. At the mangrove forest, A. cristatellus, A. pulchellus, and A. stratulus occupied sunny perches and rarely perched in shade, except at around 1200 hours.

Stomach Contents Analysis

Figure 12 shows the percent distribution of prey individuals of various lengths eaten by the Anoline species at each of the forest sites. The group of individuals, as a whole, at the high and intermediate study sites were

Consuming the relatively smaller (about 2 mn) and more frequent prey 38.

Unfortunately, the text in this section is not clear or understandable.

At station 4, the prey size of higher relative frequency was 4m. All the four frequency distributions are skewed to the right, which means that large sizes were not eaten as frequently as small ones. The mean prey lengths and the range of prey lengths utilized by the total of individuals at each of the four study sites are shown in Figure 13. The means are each very close to one another. This fact reveals some similarity among altitudinally different habitats in regard to the consumed average prey size. The ranges were determined by the largest animals at each station and these ranges do not seem to be significantly different, except for station 1. The total number of lizards found at each site was subdivided into different snout-vent length intervals; their food size selection is shown in Figure 14. In general, the frequency distributions observed at each of the four sites increased gradually from the small to the large lizards. The sample percent composition, in terms of species, the sex-classes belonging to them, and their mean sizes and percentages of variation from the high to the low study sites, are shown in Tables 10 and 11. Then, if we refer to a small lizard size-class we will probably be talking about 99% juveniles or a very small percentage of females. However, the intermediate size-class category included some young males and adult males of Amolis, as well as over 75 females, and the large size-class included only the adult males of several species.

Species. At Station 1 (Fig. 14-A), the small size-class category, which included 16% of 51 lizards, was comprised of Lizanis belonging to the 20-35 mm size interval. Their mean prey length was 2.11 mm (SD = 0.20 mm). The intermediate category, which included 588 of 31 lizards, covered sizes of 35-50 mm snout-vent length, and their mean prey length was 2.81 mm (SD = 0.60 mm). The maximum ranges are continued on the next page.

Figure 13 shows the mean of prey lengths eaten by all individuals sampled at each of the four study sites. The standard error of the means is represented by the rectangles, and the ranges are represented by the bars.

Figure 14 illustrates the means of prey lengths eaten by the different sizes of lizards sampled at each study site. The rectangles show the standard error of the means, and the bars depict the ranges. Regression lines of the prey length means are shown for each of the stations. Refer to Table 10 for the sample size of each lizard snout-vent length category.

Table 10 displays the percentages of the species' sex-classes belonging to the snout-vent length class intervals at each study site for each of the species collected as listed in Table 9.

Table 11 presents the mean sizes in millimeters and the percent variation (increase or decrease) of lizard sex classes from the highest to the lowest elevation. The lowest elevation showed the largest animals of all sites. The table is titled "Size Variation of Lizard Size & Sex by Elevation and Species

Sex".

The text provided appears to be a mix of unrelated data and a scientific study about lizards' prey. Data seems to be random numbers, symbols, and possibly incorrectly transcribed pricing or measurement information. The study part, however, can be fixed as follows:

The sizes of prey items taken by small, intermediate, and large lizards were 8, 14, and 15 mm, respectively. The large adults (50-70 mm) consumed prey with a mean length of 4.16 mm (SD = 0.87). At station 2 (Figure 14-8), small lizards (18% of 33 lizards) with a snout-vent length of 20-30 mm consumed prey with a mean length of 2.51 mm (SD = 0.10 mm). Intermediate lizards (58% of 33) with a 30-50 mm snout-vent length consumed prey with a mean length of 4.06 mm (SD = 0.67 mm). Large specimens (24% of 33), measuring between 50-65 mm, consumed prey with a mean length of 5.59 mm (SD = 2.52 mm). The maximum sizes of prey consumed by small, intermediate, and large lizards were 4, 20, and 20 mm, respectively.

At station 3 (Figure 14 - C), small lizards (53% of 45 lizards) with a snout-vent length of 16-30 mm consumed prey with a mean length of 1.89 mm (SD = 0.43 mm). Intermediate lizards (45% of 45) with a 30-50 mm snout-vent length consumed prey with a mean length of 3.06 mm (SD = 0.74 mm). Large lizards (48% of 45) with a 50-65 mm snout-vent length consumed prey with a mean length of 9.17 mm (SD = 4.01 mm). The maximum sizes of prey consumed by small, intermediate, and large lizards were, respectively, 11, 17 and 20 mm.

At station 4 (Figure 14 - D), small lizards (81% of 48 lizards) with a snout-vent length of 25-30 mm consumed prey with a mean length of 2.22 mm (SD = 0.63 mm). Intermediate lizards (50% of 48) with a 30-50 mm snout-vent length consumed prey with a mean length of 2.62 mm (SD = 0.37 mm). Large lizards (42% of 48) with a 50-80 mm snout-vent length consumed prey with a mean length of 4.19 mm (SD = 0.64 mm). The maximum sizes of prey consumed by small, intermediate, and large lizards were, respectively, 4, 16 and 22 mm.

At the... [Text ends here]

Four stations, the difference in mean prey length between small and intermediate lizards was smaller than between the intermediate and large lizards. In Figure 14, the regression curves of the means of prey lengths eaten by Anolis of different snout-vent lengths at each of the four study sites also appear. This analysis produced the following coefficients of determination: .4560 for station 1, .6185 for station 2, .0426 for station 3, and .9479 for station 4. These coefficients yield the proportion of the total variability of the dependent variable that may be assigned to the effect of the independent or causative variable (Le Clerg et al., 1962). The dependent variable in this analysis is prey length and the causative variable is lizard snout-vent length. Thus, at station 1, prey size is affected by lizard size 46% and 54% by other parameters present in the environment. Similarly, at station 2, 62% is the effect of lizard size on prey size, at station 3, 64%, and at station 4, 95%. Probably, at the mangrove forest site (4) because lizards were exposed to a relatively more abundant food supply and broader food size spectra than in the three other habitats, the selection of prey size correlated more with lizard snout-vent length. It is plausible that at the habitats with less food abundance, all lizards were forced to eat the smaller food items.

Food Availability

The frequency distributions of the available food lengths at each of the four study sites are shown in Figure 15. The means and the ranges of the maximum lengths of potential prey are displayed in Figure 16. The cumulative frequency distribution of these potential-prey sizes found at each of the four habitats appears in Figure 17. The cumulative volume distributions are also shown in Figure 18. Figure 15 A, B, C, and D shows four skewed-to-the-right relative.

The subsequent text is not clear enough to correct. Please provide a clearer version.

"See page 5 (July 19, 1937) copy (July 1, 1922) copy of STANISLAV LINGUISTIC LECTURE. Be sure to stop at the station! And be...

Frequency distributions of the food available to the Anolis species have been observed. The location of samples is biased against animal food found at tree trunks and at other vertical layers of the forest habitats. The highest percentages of the food lengths sampled at the four stations were observed to be at about 2 to 5mm. Nevertheless, station 1 appeared with 48% of 1 mm food length and 44% of 2 mm. The food lengths with the highest percentages were 46% of 2 mm at station 2, 47% of 2 mm at station 3, and 62% of 2.5 mm at station 4. The mean prey length at station 1 was 1.82 mm, at station 2 was 2.40 mm, at station 3 was 2.67 mm, and 2.67 mm at station 4. The calculated coefficients of variation (S/Z x 100) were, in respective order, 54.0, 25.3, 54.9, and 32.5%. Apparently, the ratios between their standard deviations and their means vary in a similar way at stations 1 and 3, and at 2 and 4, but, in general, the mean prey lengths at the four sites may be considered to be reliable figures that can be useful for comparison among the habitats. The smallest maximum prey length was observed at the highland habitat, and the greatest at the Tabonuco/Ausubo intermediate altitude habitat (station 2). Stations 3 and 4 showed similar maximum prey lengths. The observed maximum prey lengths at station 1, 2, 3, and 4 were, respectively, 8, 20, 12 and 10 mm (Fig. 16). The relative abundances observed at the four study sites showed heavy differences in the total frequencies between the lowland and the highland habitats. The intermediate habitats differed slightly in their total frequencies (Fig. 17). The totals at each station, from the highland to the lowland habitats, were 445, 991, 856, and 2877 items. For a 0.01 hectare, these figures yield, respectively, 99, 220, 190 and 639 items. The cumulative volume of the food items (Fig. 18) of the sites showed 48

FOOD LENGTH IN MILLIMETERS STATION Fig. 16, The means of"

"Food lengths were sampled at each of the four study sites. The standard error of the means is shown by the rectangles, and the ranges by the bars.

FREQUENCY: 3000, 2800, 2600, 2400, 2200, 2000, 1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200. Fig. 17. Station Pone Pores 310M (2 18 to 15 16 17 18 13 20). POTENTIAL PREY SIZE IN MM: The cumulative frequency distributions of the potential prey lengths sampled at the four study sites.

CUMULATIVE VOLUME: 8000, 7000, 6000, 5000, 4000, 3000, 2000, 1000. Fig. 18. Station ST 34 56789 1011 1215 141516 17 18 1920. POTENTIAL PREY SIZE IN MM: The cumulative volume distributions of the potential prey lengths sampled at four study sites.

A cumulative pattern similar to that of the cumulative frequency was observed. These volumes were estimated at all the stations: station 1 with 807 m3, station 2 with 2381 m3, station 3 with 2281 m3, and station 4 with 7681 m3. At the intermediate stations 2 and 5, the cumulative volumes were very similar. Probably, these two habitats maintain similar general climatic conditions and insect populations. These data may be biased against populations having 4 seasonal maxima at other times (e.g., week, month, or year). However, in regard to the extreme habitats, insect population maxima could have a smaller effect on the data observed than with the intermediate elevation habitats.

Climate: The climatic patterns observed at the four elevations are presented in Figure 19. The mean temperatures in degrees Celsius for stations 1, 2, 3, and 4 during the period from November to February were 18.62, 22.45, 22.00, and 26.00, respectively. The maximum extreme values were 20.11 and 25.79 for stations 1 and 2, respectively. For stations 3 and 4 no measurements were available. The minimum extreme values for stations 1 and 2 were 17.55 and 21.72°C, respectively. Among the four months of the study period, November represents the highest temperature month at each elevation. The standard errors of the means for stations 1 and..."

The temperatures at the two sites were 0.98 and 0.76°C, respectively. These resulted in low coefficients of variations of St and 38, respectively. These coefficients suggest that both sites exhibit slight and similar variations in temperature. The average rainfalls in millimeters of water for stations 1, 2, 3, and 4 during the period from November to February were 289.57, 143.03, 76.28, and 98.49, respectively. The maximum values were 378.46, 204.72, 82.

300. 2 100 ~ 1 2 3 4 stations 20 Pes we. rr) stations Fig. 19. The climatic data averaged for the temperature and rainfall recorded during the period from November to February of the previous three consecutive years; from Nov. 1974 to Feb. 1977.

The maximum values were 121.67, and 149.35 mm for stations 1 to 4, respectively. The minimum values for stations 1 to 4, respectively, were 170.18, 87.40, 27.24, and 539.12 mm. The highest monthly average at station 1 and 2 occurred during December; at station 3 during February; and at station 4 during January. The standard errors of the means for stations 1 to 4 were, respectively, 90.33, 62.98, 40.17, and 45.74 mm. These standard errors yield the following coefficients of variation in respective order: 31, 44, 53, and 46%. These percentages suggest that rainfall is more variable than temperature at each of the study sites, and that the rainfall data of the averaged period was less variable at station 1 and 2 than at the other elevations. However, the temperature data was more constant from month to month during the averaged three-year period at each site.

Species Diversity

In Table 12, the diversity indexes of the lizard and tree species found at each of the forest habitats are shown. The observed patterns indicate that as the tree index increased, the lizard index also increased, except at the mangrove forest site where there was only one tree species, and therefore, zero diversity. But this fact is not as important, particularly to the arboreal genus Anolis of ectothermic animals, as is the number of different microhabitats existing at each site.

Habitat, regardless of the tree species diversity, the tree composition, and age of every habitat could have a cause-and-effect relationship with the availability of surface areas and the number of microclimates available to these lizards. The number and area of microhabitats are shown in Table 13-A, which displays the areas in square meters available to the anoles as their potential structural and climatic microhabitats.

Table 12: The diversity of the Anolis and tree in four forest habitats.

SPECIES DIVERSITY INDEX

Organisms	Stations			
	1	2	3	4
Lizards	0.64	1.35	1.76	1.42
Trees	1.93	3.01	2.16	0.00

Table 13: The estimated cover area of the potentially available microhabitats at the four forest habitats.

A. The structural microhabitat cover in square meters;

B. The microclimate cover in square meters.

The ground area of each study site is 450 m.

The greatest trunk surface area availability occurred at station 2 and the least at station 4. Also, the least understory vegetation area occurred at station 2, along with the greatest leaf and wood litter cover. However, larger understory vegetation areas occurred at stations 1 and 3.

At station 4, the mangrove seedlings of about 10 cm high were included within the leaf and wood litter category, since these were not found intermingled with grasses or saplings of more than 30 cm high. At station 1, the understory vegetation cover was composed of ferns, mosses, liverworts, bromeliads, very short Sierra palms (Prestoea montana), and Canasey species, among other plants. At station 2, almost no understory vegetation was growing, except for a few Prestoea montana saplings. At station 3, the understory vegetation was denser than at station 1, but did not cover as much area.

The area is as in the former station. The leaf and wood litter at all stations was composed of the debris dropped by the tree species listed in Tables 1-4. The available microclimatic areas (microclimates) shown in Table 15-B indicate the existence of a number of different climatic regions under the canopies of the four forest sites. Each forest site showed a distinct composition of lizard species according to this. Furthermore, elevation determined which morphological counterpart species would replace the other at a different microclimate. Thus, a highland species like A. gundlachi was found in the shade, while the lowland species A. cristatellus (i.e., its morphological counterpart) was found in the sun with remarkably greater frequency. During a sunny day, the most shaded microhabitat was found at station 2. The sunnier microhabitats, during this similar weather condition, were found at station 3 and 4. The degree of sunlight penetration at station 1 (near the cloud forest) at a given time depended upon the speed, movement, and size of the cloud formations. During November (and in the earlier summer and autumn months) and through December, the Prestoea montana palm brake, and most of the Luquillo Mountain Range peak tops, were covered by clouds. Thus, the sunnier microclimates were observed (along the altitudinal cline) at the lower elevations, where temperatures were higher, than at the higher elevations. As mentioned before, A. gundlachi was observed about 12% in the sunlight at stations 1 and 2, but the temperatures at these elevations were considerably lower than at the lowlands. Also, this species was found in the relatively less sunny microclimates at station 3 where temperatures were hotter.

Discussion

The levels of population density of the Anolis Lizards studied in the watershed of the Rio Espiritu Santo may be influenced by the hypothetical ecological parameters related to the climatic preference (Table 9); the selection of different combinations of perch diameter and height (Table

study discusses the following aspects: the available surface area of the different structural microhabitats (Figures 8, 10, and 11); the patterns of spatial distribution of individuals on the study sites (Figure 9); and the food size availability and selection by the anoles (Figures 12-18). The predators of the Anolis species found in the watershed (e.g., birds, rats, mongooses, snakes) were not included in the present work, but some of these have been documented elsewhere (Wetmore, 1916; Odum, 1970). It is plausible that to avoid heavy competition, the natural populations of Anolis Lizards tend to maintain certain density levels according to the available resources at a given habitat. This is believed to be the result of natural selection and the ecological adaptations of the species throughout the long-term evolutionary process. The available food of the Anolis lizards is shared by other consumers belonging to the food webs of the forest habitats. Thus, the number of individuals might also be regulated by the partitioning of a common food source. From the stomach content analysis, a plausible statement is that the anoline species are found close to the top of the food chains of these habitats. In addition, these analyses indicate that the food size spectra available in the field were broadly utilized by the anoles since both food and prey distributions were very similar. However, it is not known if the available food items at the study sites are sufficient to maintain an even greater lizard abundance. Hypothetically, some other ecological factors existing at a specific site, including parasitism and predation, might be stressing the anoles at different stages of their life cycle, otherwise, the population number might be maintained at a higher level. Unfortunately, there are no data on parasitism and predation for these species populations, since these parameters are in fact very difficult to estimate. In the final analysis, although many aspects about the ecology of Anolis populations are unknown, the present

The study documents that at sites with greater food abundance (i.e., lowlands), the lizard abundance and density were also greater. Furthermore, the relative densities of individual species seem more difficult to interpret than the total density of the entire community. This is because the variation in the number of individuals of a given species from one elevation to the next may be determined by many more limiting factors (i.e., climatic, microclimatic, structural, behavioral-territorial, interspecific interactions as well as intraspecific, food availability, predators).

However, the total number of individuals, regardless of species, would ultimately be determined by the community.

Thus, the variation in lizard relative densities along an altitudinal cline suggests that food and structure availability play important roles in the existence of natural populations of Anolis as a whole. However, water availability may also regulate anoline life histories by causing egg or juvenile mortality, as seen with populations of Anolis acutus on St. Croix, U.S. Virgin Islands (Reisbal and Philibosian, 1974), and Anolis limifrons in Panama (Sexton, 1967).

The study sites of this paper do not seem to differ significantly from each other in terms of water or moisture availability during the wet season, which could negatively affect eggs or juveniles. Moreover, water availability plus higher temperatures in the lowlands may be the combination of parameters positively affecting the reproductive cycles of insects, and thus, food abundance.

The relative population densities of Anolis species on Puerto Rico included in the present study compare satisfactorily with the results of similar studies. In Panama, A. limifrons showed a density of 0.03 lizards/m2 (Sexton et. al., 1963; Sexton, 1967). The density of A. rebulosus in Mexico (Jenssen, 1970) was shown to be 0.06-0.09 lizards/m2. A. acutus on St. Croix (U.S., Virgin Islands) had 0.43 lizards/m2 which is an exceptional case.

Population density for the genus (Ruibal and Philibosian, 1974). 'Anolis pulchellus' in Puerto Rico was estimated at 20,000 per hectare (Gorman and Harwood, 1977), or about 2 lizards/M2. Ecological aspects of the Anolis species of the four forest habitats: The data on surface availability suggest that if a greater trunk surface area and number of trees would more likely occur at a given site than at another, then, whenever there exists a relatively higher frequency of lizards at this hypothetical habitat, its relative density would comparatively increase too. The food relative abundance increases from the higher to the lower elevations of the study as mentioned earlier. From this, it is plausible that at the mangrove habitats of the northeastern coastal plains (i.e., sites with a relatively greater lizard density) a population of lizards may increase to a greater abundance of individuals than at a highland habitat of greater surface area, but with a lower food relative abundance. The microhabitat differences shown by the Anolis species may result in an increment in the number of lizards at a site, provided there is enough food. The available food sizes, which are also believed to have been randomly distributed on the ground, were known (Figs. 15 and 17) to have been selected by the total number of lizards at every single one of the four study sites as mentioned before. Indeed, the prey size distribution was selected by the lizards perching close to the ground but, at varying heights and diameters above it (Figs. 10 and 11). This might be a mechanism among the syntopic species for reducing competition or to, perhaps, avoid it. Thus, there is evidence supporting the facts that 1) the available food size spectra were consumed by the anoline lizards, and 2) that the food abundance may have a regulatory impact on the total number of Anolis individuals at all the four habitats. A low lizard abundance would occur at a high elevation habitat relatively cold, wet, and with a low food relative abundance.

Rather than at a low elevation habitat, specifically a mangrove forest, which is relatively hot, wet, and food-rich, supporting a relatively higher lizard abundance.

The individuals of most natural populations usually occur in randomly distributed groups or clumps. In regard to the Anolis of this study, the intermediate-elevation and lowland species appeared in groups of 2, 5, or 4 lizards. The highest number of lizards perching together with other lizards on some of the trees at a site was observed at station 4, the lowland mangrove habitat. This pattern varied along the line more, perhaps, as a function of food availability than of surface availability.

If at a similar lowland habitat food items would also occur in relatively large quantities (which is highly probable) and, in addition, surface area were found to be higher than at station 4, the density of lizards on the trees should tend to increase too. The total abundance of lizards is also expected to increase at a habitat with these hypothetical conditions.

Recommendations for future studies on the ecology of Anolis lizards include 1) the assessment of a lowland habitat similar to the mangrove forest habitat studied in the present work in relation to the physical parameters of surface area and number of trees, and to the biotic parameter of food availability; and 2) the assessment of Anolis population density at El Verde forest habitats selected at the same altitudes that the present study sites were selected. These two future assessments should yield valuable and interesting comparative data to corroborate the present findings.

Literature Cited

Andrews, R. M. 1971. Structural habitat and time budget of a tropical ‘Anolis lizard. Ecology 52(2): 262-270.

Andrews, R. M. 1976. Growth rate in island and mainland anoline lizards. Copeia 1976: 477-482.

Center for Energy and Environment Research. Weather data from the Environmental Sciences Division. Medical Center-University of Puerto Rico, Rio Piedras, Puerto Rico.

Collette, B. B. (1961). Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. Bull. Mis. Comp. Zool, 125(5), 137-163.

Dobzhansky, T., & Pavan, C. (1950). Local and seasonal variations in relative frequencies of species of Drosophila in Brazil. J. Anim. Biol, 19, 1-14.

Fitch, H. S. (1972). Ecology of Anolis tropidelopis in Costa Rican cloud forest. Herpetologica, 28, 10-21.

Gorman, G. C., & Atkins, L. (1967). The relationships of Anolis of the roquet species group (Sauria: iguanidae). II. Comparative chromosome cytology. Syst. Zool, 16, 137-145.

Gorman, G. C., & Atkins, L. (1969). The zoogeography of Lesser Antillean Anolis Lizards: an analysis based upon chromosomes and lactic dehydragenase. Bull. Museum Comp. Zool, 138, 53-80.

Gorman, G. C., & Harwood, R. (1977). Notes on population density, vagility, and activity patterns of the Puerto Rican grass lizard, Anolis pilcheius (Geptilia, Lacertilia, Iguanidae). J. Herp, 11(3), 363-368.

Gorman, G. C., & Licht, P. L. (1974). Seasonality in ovarian cycles among tropical Anolis lizards. Ecology, 55, 360-369.

Gorman, G. C., Thomas, R., & Atkins, L. (1968). Intra-and interspecific Chromosome variation in the lizard Anolis cristatellus and its closest relatives. Breviora Mis. Comp. Zool, 295, 1-15.

Jenssen, J. A. (1970). The ethoecology of Anolis nebulosus (Sauria, Iguanidae). J. Herpetol, 4, 1-38.

Le Clerg, E., Leonard, W. H., & Clark, A. G. (1962). Field Plot Technique (2nd ed., p. 83). Burgess Publishing Company.

Levins, R., & Heatwole, H. (1963). On the distribution of organisms on islands. Carib. J. Sci, 3, 173-177.

Licht, P. (1974). Response of Anolis lizards to food supplementation in nature. Copeia, 1974, 215-221.

Licht, P., & Gorman, G. C. (1970). Reproductive and fat cycles in Caribbean Anolis lizards. Univ. Calif. Publ. Zool, 95, 1-52.

Licht, P., & Gorman, G. C. (1975). Altitudinal effects on the seasonal testis cycles of Tropical Anolis lizards. Copeia, 1975, 496-504.

Lugo, A. E. (1970). Photosynthetic studies on four species of rain forest seedlings. In A Tropical Rain.

"Forest, A Study of Irradiation and Ecology at El Verde, Puerto Rico" by H. T. Odum (Ed.), pp. I-81-T-102, Division of Technical Information, U.S. Atomic Energy Commission. Margalef, R, 1965. "Perspectives in Ecological Theory," University of Chicago Press, Chicago, 112 pp. National Oceanic and Atmospheric Administration, Aeropuerto Internacional de Isla Verde, Isla Verde, Puerto Rico. Odum, E. 1971, "Fundamentals of Ecology," 3rd ed., p. 268, Saunders. Odum, H. T. 1970, "A Tropical Rain Forest, A Study of Irradiation and Ecology at El Verde, Puerto Rico," H. T. Odum (Ed.), Division of Technical Information, U.S. Atomic Energy Commission. Rand, A. S. 1964, "Ecological Distribution in Anoline Lizards of Puerto Rico," Ecology 45:745-752. 1967, "Ecology and Social Organization in the Iguanid Lizard Anolis Tineatopus," Proc. U.S. Nat.-Mus. 122:1-79. Ruibal, R. 1961, "Thermal Relations of Five Species of Tropical Lizards," Evolution 15:98-111. Ruibal, R. and R. Philibosian. 1974, "The Population Ecology of the Lizard Anolis Acutus," Ecology 55:525-537. Schmidt, K. P. 1928, "Amphibians and Land Reptiles of Porto Rico, with a List of Those Reported from the Virgin Islands," Scientific of Porto Rico and the Virgin Islands, N. Y. Acad. Sciences #10:1-160. Schoener, T. W. 1967, "The Ecological Significance of Sexual Dimorphism in Size in the Lizard Anolis Conspersus," Science 155:474-476. 1968, "The Anolis Lizards of Bimini: Resource Partitioning in a Simple Fauna," Ecology 49:704-726. 1970, "Size Patterns in West Indian Anolis Lizards: II. Correlations with the Size of Particular Sympatric Species, Displacement and Convergence," Amer. Nat. 104:155-174.

Schoener, T. W. and G. C. Gorman, 1968. "Some Niche Differences among Three Species of Lesser Antillean Anoles," Ecology 49:819-830. Schoener, T. W. and A. Schoener. 1971a, "Structural Habitats of West Indian Anolis Lizards: I. Lowland Jamaica," Breviora 368: 1-537. 1971b, "Structural Habitats of West Indian Anolis Lizards, Puerto Rican Uplands," Breviora 375:1-39. Sexton, O.

J. 1967. Population changes in a tropical lizard Anolis Limifrons on Barro Colorado Island, Panama Canal Zone, Copela 17219. Sexton, O. J., J. Bauman, and E. Ortleb. 1972. Seasonal food habits of Anolis limifrons. Ecology 53:182-186. Sexton, O. J., H. F. Heatwole, and E. H. Meseth. 1963. Seasonal changes in the Lizard Anolis Limifrons in Panama, Am. Midl. Nat. 69:482-491. Shannon, C. E., and W. Weaver. 1963. The mathematical theory of communication. University of Illinois Press, Urbana. 117 pp. Stejneger, L. 1904. The herpetology of Porto Rico. Rept. U. S. Nat. Mus. 1904:581-720. Wetmore, A. 1916. Birds of Puerto Rico. U.S. D.A. Bull. 326. 140 pp. Williams, E. E. 1969. The ecology of colonization as seen in the geography of anoline lizards on small islands. Q. Rev. Biol. 44:345- 365.