

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 Río Espíritu Santo was assessed by means of daily counts of the individuals. Besides 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 (station 3) the Roble Blanco forest site. 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 (station 4) the mangrove forest site. The stomach content analyses showed that the available food was selected by the lizards. The frequency distributions of available food sizes was 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 giving statistical advise and laboratory facilities, Elvira Cuevas for her help with the study proposal, George C. Gorman and Robin M. Andrews for their preliminary advise and discussion, Francisco D. Folch Castañer commented on the laboratory and field data, Alejo Estrada Pinto and Juan Martínez 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 for supplying weather data, and Manuel J. Vélez and Gustavo Candelas for their comments on the final draft.

Also José Colón provided his field equipment, Miguel Canals, Félix 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 Rodríguez typed the final report.

I truly thank Provi Seín for her support, understanding, and help.

TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION.....	1
Previous Studies on the Ecology of <u>Anolis</u>	2
MATERIALS AND METHODS.....	5
Study Sites.....	5
Location and Floristics.....	5
Spatial Distribution of Trees.....	7
Climate.....	7
Lizards.....	13
Relative Abundance Census.....	13
Spatial Distribution.....	14
Structural Habitat.....	14
Climatic Habitat.....	15
Stomach Contents Analysis.....	15
Body Size.....	16
Food Availability.....	16
Surface Availability.....	16
Index of General Species Diversity.....	17
Number and Area of Microhabitats.....	18
RESULTS.....	19
Lizards.....	19
<u>Anolis</u> Relative Abundance.....	19
The Zonation Patterns of <u>Anolis</u> Lizards.....	25
Structural Habitat Selection.....	28
Climatic Habitat: Sun or Shade Selection.....	36

	<u>Page</u>
Stomach Contents Analysis.....	38
Food Availability.....	46
Climate.....	52
Species Diversity.....	54
Number and Area of Microhabitats.....	54
DISCUSSION.....	58
Ecological Aspects on the Anolis Species of the Four Forest Habitats.....	60
LITERATURE CITED.....	63

LIST OF TABLES AND FIGURES

<u>Table</u>	<u>Page</u>
1. List of tree species found in the Sierra Palm forest site (station 1) where 118 trees were considered for the tree species diversity calculations.....	9
2. List of tree species found in the Tabonuco forest site (station 2) where 72 trees were considered for the tree species diversity calculations.....	10
3. List of tree species found in the Roble Blanco secondary succession forest site (station 3) where 127 trees were considered for the calculation of tree species diversity.....	11
4. The only tree species found in the Mangrove forest site (station 4). The total number of individual trees was 53. Some patches of grass were found mixed with this tree species.....	11
5. Relative abundance of each sex class in every lizard species found at different altitudes in the topography of Río Espíritu Santo watershed.....	22
6. Lizard relative density expressed in terms of <u>Anolis</u> relative abundance per: 1) tree, 2) m ² of topographical area, 3) m ² of tree surface, and 4) m ² of total available surface (ground and tree). Values are 1×10^{-2}	24
7. Perch availability in each of the four study sites expressed in terms of m ² of surface: area of ground - tree basal area = available ground area, + surface of tree trunks.....	24
8. The different combinations of perch height and perch diameter utilized by the <u>Anolis</u> species sex/size classes (juveniles, females, and males) at each station. The combinations are given in percents of the total of individuals belonging to each one of the species' classes. These totals appear to the left of the sex-class categories.....	29
9. The microclimates of the <u>Anolis</u> species found at the four forest habitats shown in percents. The numbers in parenthesis are the total observations for each species at the given site.....	37
10. The percentages of the species sex-classes belonging to the snout-vent length class intervals at each one of the study stations: E, G, S, Cr, K, P, stand for each of the species collected for stomach contents analysis as in Table 9; J, F, M, represent the sexes. The asteriks are young adult males..	43

<u>Table</u>	<u>Page</u>
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.....	44
12. The diversity of the <u>Anolis</u> and tree species found at the four forest habitats.....	55
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 ²	56

<u>Figure</u>	<u>Page</u>
1. The general area of the study in the northwestern region of the Luquillo Mountains. This map was adapted from a U.S.G.S. map 1976.....	6
2. Elevation profile ranging from the mouth of Río Espíritu, up El Verde Area, to 884 m. near Mt. Britton.....	8
3-6. The spatial distributions of the large and small trees (see text) found at stations 1-4, respectively.....	12
7. The <u>Anolis</u> relative abundance observed from the highland habitat (1) and along the altitudinal cline to the lowland habitat (4) in the Río Espíritu Santo watershed. The elevation curve shows the X's and the relative abundance curve shows the O's.....	20
8. The <u>Anolis</u> 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 legend at right corner for species' symbols.....	21
9. The lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D).....	26
10. The percent of observations of the <u>Anolis</u> perch height distributions at each forest habitat. Percentage is of total for each sex class/species over range of perches. The symbols j, f, m, indicate juveniles, females, and males, respectively.....	33
11. The percent of observations of each <u>Anolis</u> species at every study site showing the utilized perch diameters.....	34

<u>Table</u>	<u>Page</u>
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.....	44
12. The diversity of the <u>Anolis</u> and tree species found at the four forest habitats.....	55
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 ²	56

<u>Figure</u>	<u>Page</u>
1. The general area of the study in the northwestern region of the Luquillo Mountains. This map was adapted from a U.S.G.S. map 1976.....	6
2. Elevation profile ranging from the mouth of Río Espíritu, up El Verde Area, to 884 m. near Mt. Britton.....	8
3-6. The spatial distributions of the large and small trees (see text) found at stations 1-4, respectively.....	12
7. The <u>Anolis</u> relative abundance observed from the highland habitat (1) and along the altitudinal cline to the lowland habitat (4) in the Río Espíritu Santo watershed. The elevation curve shows the X's and the relative abundance curve shows the O's.....	20
8. The <u>Anolis</u> 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 legend at right corner for species' symbols.....	21
9. The lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D).....	26
10. The percent of observations of the <u>Anolis</u> perch height distributions at each forest habitat. Percentage is of total for each sex class/species over range of perches. The symbols j, f, m, indicate juveniles, females, and males, respectively.....	33
11. The percent of observations of each <u>Anolis</u> species at every study site showing the utilized perch diameters.....	34

<u>Figure</u>	<u>Page</u>
12. The percent relative frequency distribution of the prey lengths found in the stomach contents of all the <u>Anolis</u> lizards captured. A. The distribution at station 1; B. The distribution at station 2; C. The distribution at station 3; D. The distribution at station 4.....	39
13. 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...	41
14. 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 the ranges. Regression lines of the prey length means are shown for each of the stations. See Table 10 for the sample size of each lizard snout-vent length categories.....	42
15. The percent relative frequency distributions of the potential-prey lengths sampled at the four study sites.....	47
16. The means of food lengths 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.....	49
17. The cumulative frequency distributions of the potential-prey lengths sampled at the four study sites.....	50
18. The cumulative volume distributions of the potential-prey lengths sampled at the four study sites.....	51
19. The climatic data 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.....	53

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 regimes (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-e.g., 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 anoline species living at high, intermediate, and low elevations. The most relevant of these hypotheses is: that these species show altitudinal variation in 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 large 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 have been done on the ecology and morphology of this genus in tropical and subtropical, mainland and island situations. Stejneger (1904) and Schmidt (1928) 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 Andrews (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, 1963). 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 5 mm

mean prey size eaten by these Anolis species, a value not significantly different from the mean food length available at these 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 (Gorman and Licht, 1974; Licht and Gorman, 1975). In winter daylength is shorter and temperature is cooler resulting in 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 Anolis breeding season when temperatures show an average increase, though lizards show response to these little variations. As more energy is channeled into reproduction, fats can not 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 Gorman, 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, Fitch (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 Río Espíritu Santo (Fig. 1) beginning near the headwaters southwest of El Yunque Peak

ending in the estuary east of the town of Río Grande (Fig. 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 (Dacryodes excelsa/Manilkara bidentata) forest at 410 m, a Roble Blanco (Tabebuia heterophylla) forest at 250 m, and a Mangle Blanco (Laguncularia racemosa) forest at approximately 1 m. Tables 1-4 show the tree species composition, their relative frequencies, and the total of trees in each of the latter sites. In every one of these, 450 m² 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.

Spatial Distribution of Trees

All trees greater than 2.5 cms 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 Canóvanas (18°24'N, 66°54'W, nominal) at 8.5m and El Verde, Río Grande (18°21'N, 65°49'W, nominal) at 60.9 m were utilized as estimates of temperature and rainfall at the Río Espíritu 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 author. The data from CEER weather network recorded for temperature and rainfall

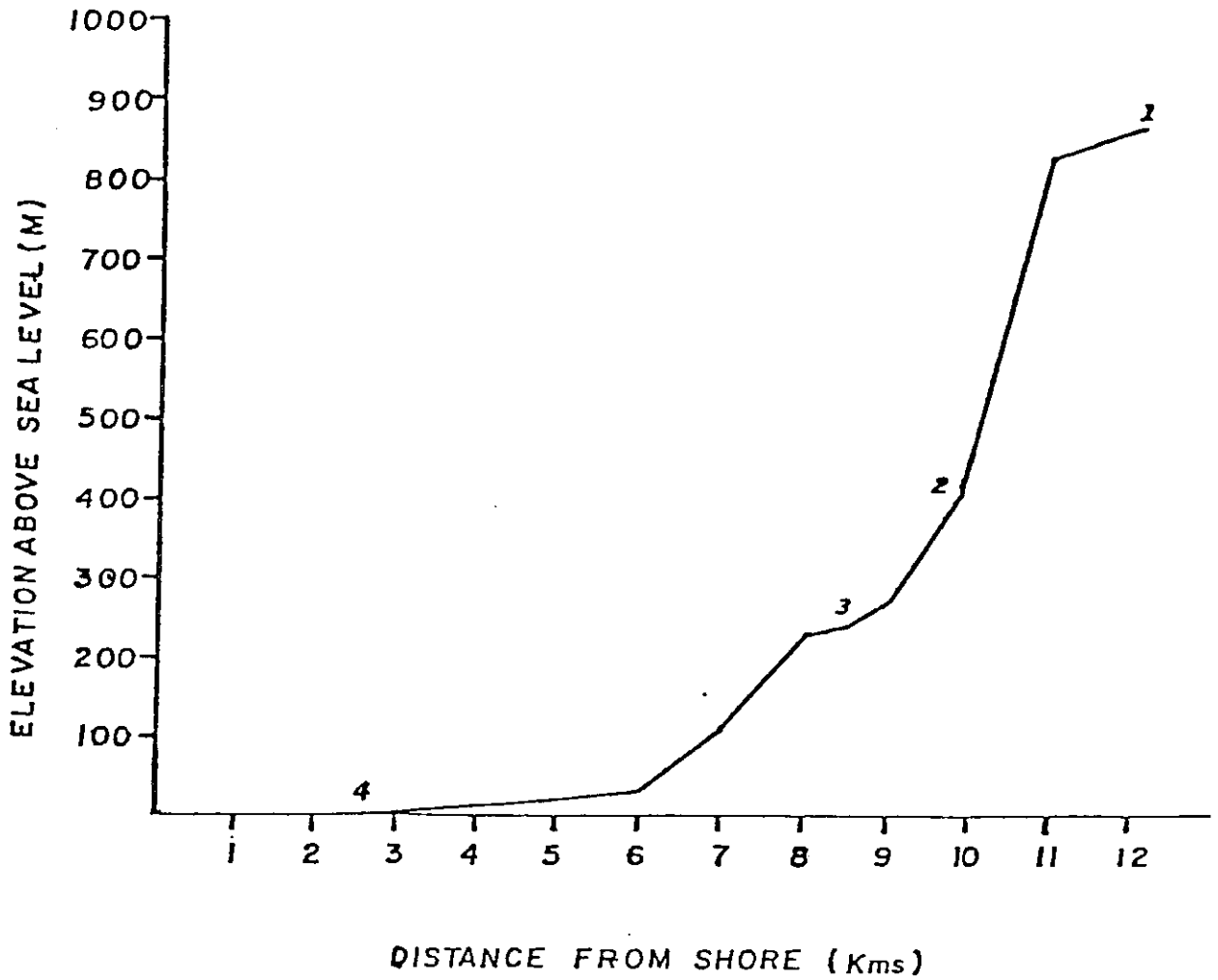


Fig. 2. Elevation profile ranging from the mouth of Río Espiritu Santo, up El Verde Area, to 884 m near Mt. Britton.

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

<u>Tree Species</u>	<u>Relative Frequency</u>
<u>Prestoea montana</u>	0.64
<u>Calycogonium squamulosum</u>	0.15
<u>Psychotria berteriana</u>	0.08
<u>Eugenia borinquensis</u>	0.03
<u>Cecropia peltata</u>	0.02
<u>Miconia guianensis</u>	0.02
<u>Alsophila bryophila</u>	0.01
<u>Ardisia glauciflora</u>	0.01
<u>Citharexylum caudatum</u>	0.01
<u>Clusia gundlachii</u>	0.01
<u>Cordia borinquensis</u>	0.01
<u>Micropholis garciniaefolia</u>	0.01
<u>Myrcia splendens</u>	0.01
<u>Tabebuia rigida</u>	0.01

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

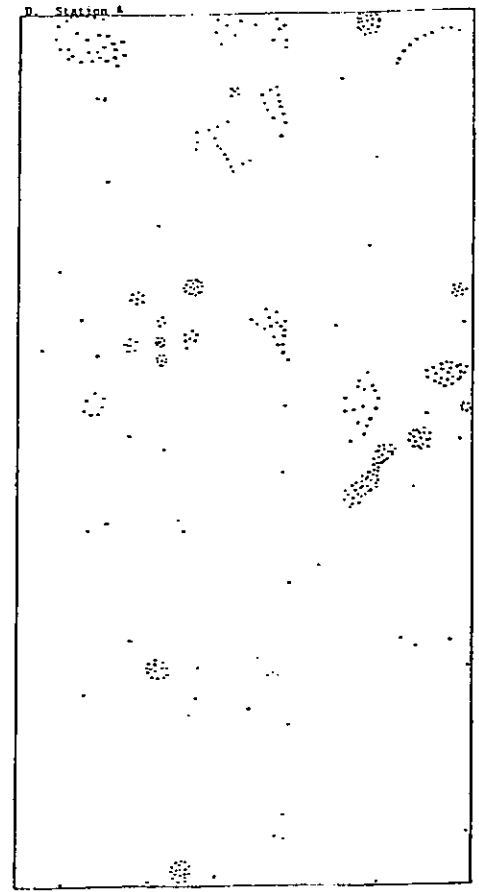
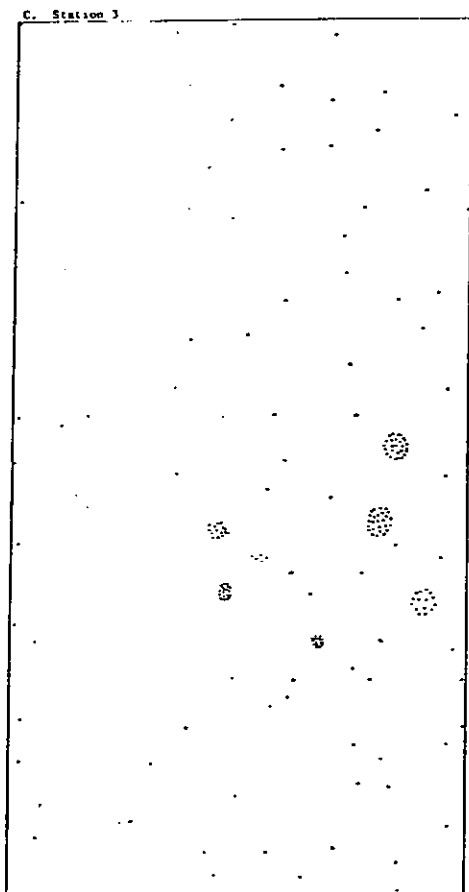
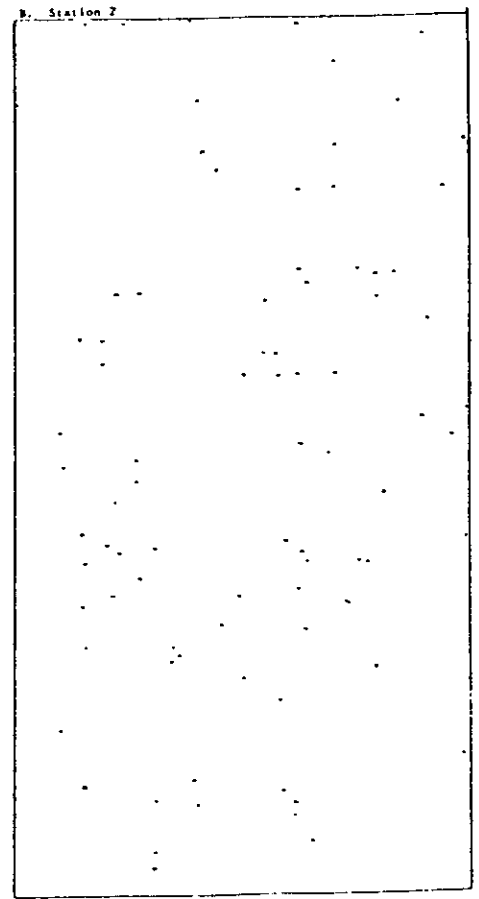
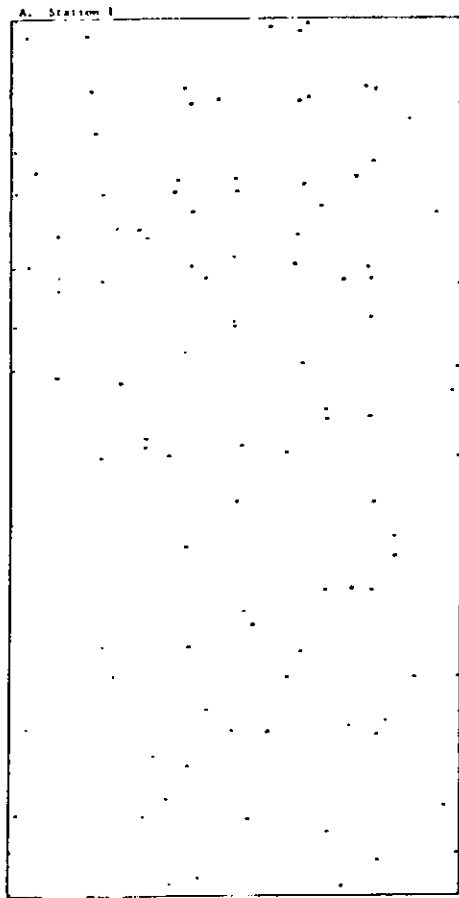
<u>Tree Species</u>	<u>Relative Frequency</u>
<u>Manilkara bidentata</u>	0.25
<u>Dacryodes excelsa</u>	0.24
<u>Prestoea montana</u>	0.15
<u>Sloanea berteriana</u>	0.13
<u>Guarea trichilioides</u>	0.06
<u>Guatteria caribea</u>	0.04
<u>Tetragastris balsamifera</u>	0.03
<u>Trichilia pallida</u>	0.03
<u>Andira inermis</u>	0.01
<u>Alchorneopsis portoricensis</u>	0.01
<u>Cassipourea guianensis</u>	0.01
<u>Guarea racemiflora</u>	0.01
<u>Myrcia deflexa</u>	0.01
<u>Ocotea moschata</u>	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.

<u>Tree Species</u>	<u>Relative Frequency</u>
<u>Tabebuia heterophylla</u>	0.62
<u>Myrcia splendens</u>	0.09
<u>Psychotria berteriana</u>	0.07
<u>Inga laurina</u>	0.05
<u>Casearia sylvestris</u>	0.03
<u>Didymopanax morototoni</u>	0.03
<u>Palicourea crocea</u>	0.03
<u>Nectandra sintenisii</u>	0.02
<u>Miconia prasina</u>	0.02
<u>Cyathea arborea</u>	0.01
<u>Myrcia deflexa</u>	0.01
<u>Prestoea montana</u>	0.01
<u>Swietenia macrophylla</u>	0.01

Table 4. This was the only tree species found in the studied mangrove forest site. The total number of individual trees was 53. Some patches of grass were found mixed with this tree species.

<u>Tree species</u>	<u>Relative Frequency</u>
<u>Laguncularia racemosa</u>	1.00



Figs. 3(A), 4(B), 5(C), 6(D). The spatial distribution of the large and small trees found at stations 1 to 4, respectively.

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, including November, December, January, and February, were averaged for three consecutive years. The rainfall and temperature patterns observed during the study period in the four habitats might shed some light on 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 microhabitats, although 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 brake. Each species sex classes were counted at regularly spaced time intervals. Sex classes will be defined in terms of body length below. A total of 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. But, for other purposes (e.g., lizard activity patterns) this way of calculating would 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 below under Surface Availability.

Spatial Distribution

One of the various kinds of data collected at the time an individual lizard was first seen, was its location on a tree perch. Each day depicts a spatial distribution pattern. For this purpose, an activity period has been chosen from each habitat. The criterion employed was the degree of activity during the period that could show the structural habitat partitioning on a horizontal level, e.g. zonation, without taking into account stratification. Thus, one of the most active periods at each site was selected.

Structural Habitat

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

Climatic Habitat

Anolis lizard species have different climatic adaptations. As a result of these adaptations these species occupied sunny and shady areas, and often intermediate zones. These data were also gathered at the time lizards were first seen 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 added separately and expressed in relative frequency percents.

Stomach Contents Analysis

Lizards are usually active during the whole day with a few exceptions. Also, they become active early in the morning as they warm up to their optimum 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 active in the 450 sq. m. around 1200 hours.

The collected animals were immediately killed with a small dose of 10% formalin. The peritoneal cavity was then filled with Turttox Insect Preservative to preserve stomach contents. I never injected 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. 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, 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 ldm² sticky traps at 1200 hrs. for a 24-hour period. Arthropods, including several orders of insects, were captured on a 2 mm-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.

Surface Availability

Anolis lizards utilize different portions of the habitat according to their morphology and physiology. Thus, the total available surface area

was estimated for each of the four forest habitats. The total includes site area minus basal area equals ground surface plus surface area of tree trunks. The basal area is the cross-section area of the trunks or approximately the area of a circle. The surface area of tree trunks was roughly estimated by calculating the area of the cylinder (e.g., the trunk), where the height and diameter of the tree were utilized.

Index of General Species Diversity

The formula used is Shannon's:

$$H = - \sum_i (n_i/N) \log (n_i/N)$$

or

$$H = - \sum_i P_i \log P_i$$

where, P_i represents the importance probability for each species (n_i/N), N equals the total of individuals in the study site, and n_i are the

individuals belonging to each species (Shannon and Weaver 1963; Margalef, 1968).

Number and Area of Microhabitats

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 50 9 sq. m. (or 3m x 3m) subplots. The density of the forest canopy and the development of an understory vegetation has a cause-and-effect relation 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 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 - absolutely defined by a dense shade microclimate with almost no sunflecks; 2) intermediate, semiclosed canopy - defined here by opened canopy/closed canopy <1 ; and 3) sunny, semiopened 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 micro-climatic category.

Results

Lizards

Anolis Relative Abundance

The lizard relative abundance data are presented in Figure 7 and 8. Figure 7 shows the total number of individuals per day at each site. An increase was observed from station 1 to 3 and a decrease from 3 to 4, but to a greater relative frequency than in station 2 at 410 m. The frequencies at stations 1, 2, 3, and 4 were, respectively, 31, 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 5 A. evermanni; station 2, 19 A. gundlachi, 22 A. evermanni; 2 A. stratulus, and 1 A. cuvieri; and at station 3, 35 A. gundlachi, 9 A. evermanni, 6 A. stratulus, 5 A. krugi, and 5 A. cristatellus. At station 4, evidently, A. gundlachi, A. evermanni, 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 Río Espíritu 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

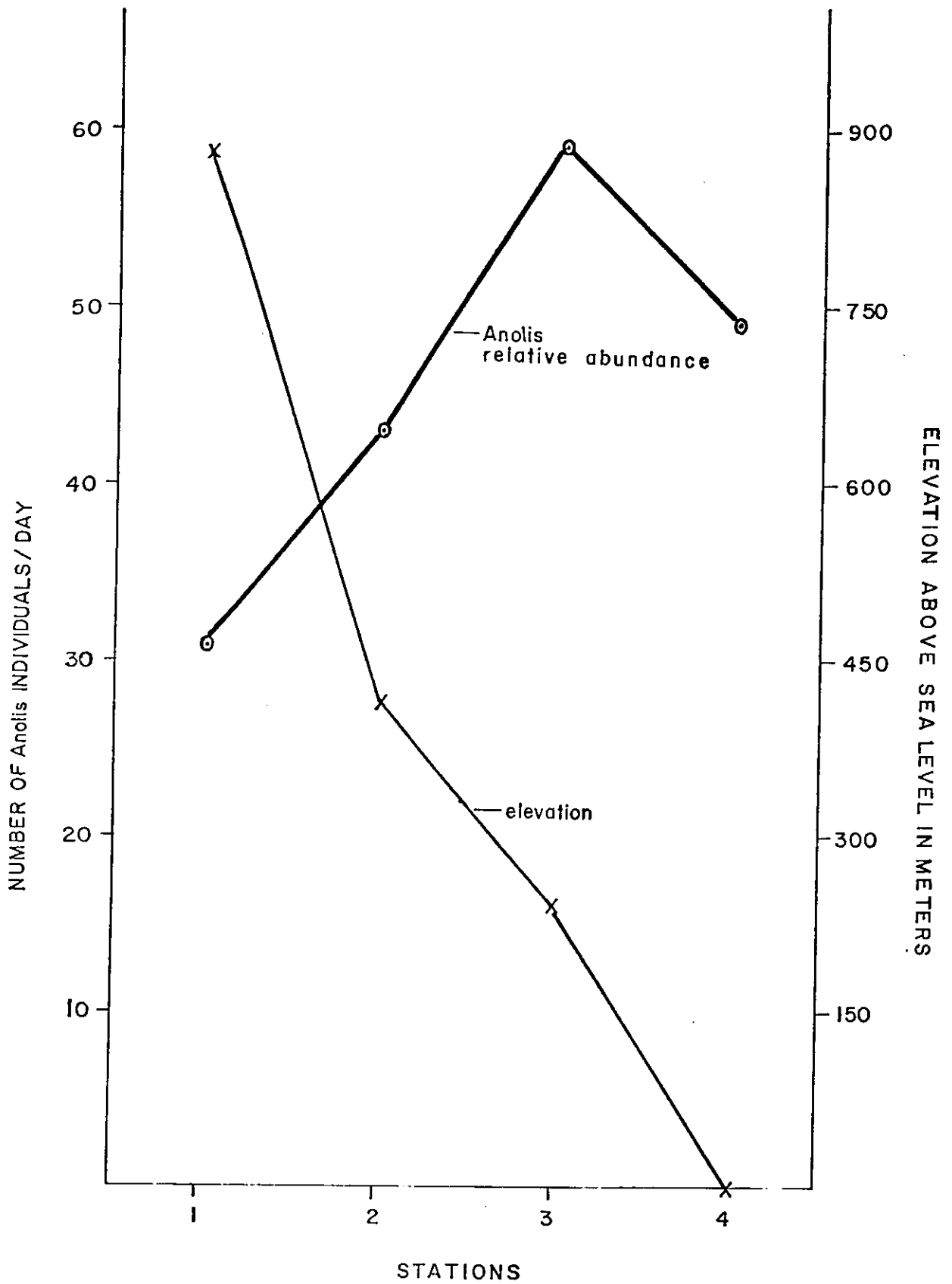


Fig. 7. The Anolis relative abundances observed from the highland habitat (1) and along the altitudinal cline to the lowland habitat (4) in the Río Espíritu Santo watershed. The elevation curve shows the X and the relative abundance curve shows the O.

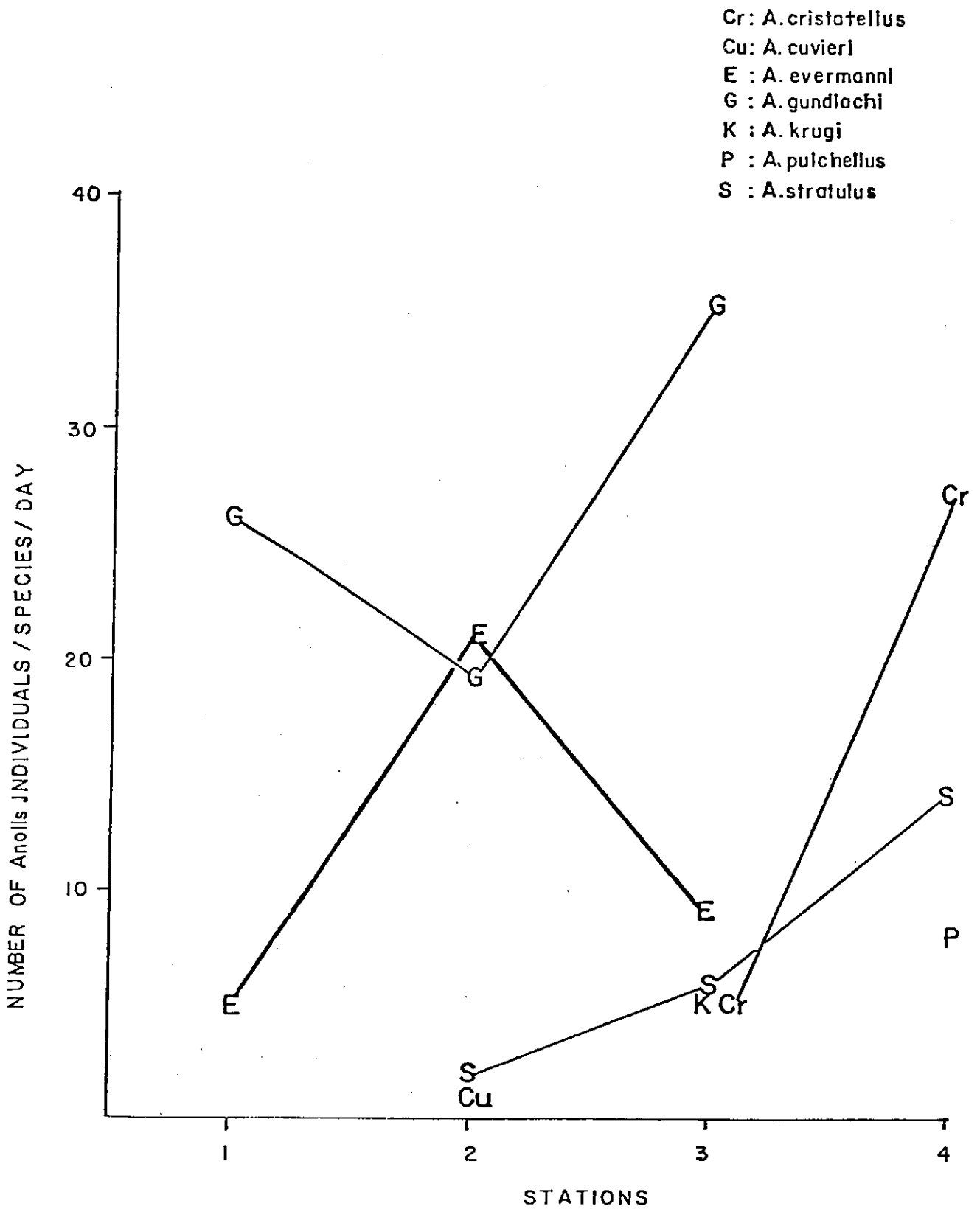


Fig. 8. The *Anolis* relative abundances of each of the species found at the four habitats. The difference in relative abundance from one station to the next is shown by the segments. See legend at right corner above for species' symbols.

Table 5. Relative abundance of each sex class in every lizard species found at different altitudes in the topography of Río Espiritu Santo watershed.

RELATIVE ABUNDANCE VARIATION OF LIZARD SIZE AND SEX CLASS INTERVALS

SPECIES	SEX	STATIONS							
		1	%	2	%	3	%	4	
G	J	7	-57.14	3	66.67	5	-	-	
	F	14	-28.57	10	100.00	20	-	-	
	M	5	20.00	6	66.67	10	-	-	
E	J	2	200.00	6	-50.00	3	-	-	
	F	2	400.00	10	-60.00	4	-	-	
	M	1	500.00	6	-66.67	2	-	-	
S	J	-	-	1	00.00	1	00.00	1	
	F	-	-	1	300.00	4	00.00	4	
	M	-	-	-	-	1	800.00	9	
Cu	J	-	-	1	-	-	-	-	
	F	-	-	-	-	-	-	-	
	M	-	-	-	-	-	-	-	
K	J	-	-	-	-	2	-	-	
	F	-	-	-	-	2	-	-	
	M	-	-	-	-	1	-	-	
Cr	J	-	-	-	-	2	-50.00	1	
	F	-	-	-	-	2	750.00	17	
	M	-	-	-	-	1	800.00	9	
P	J	-	-	-	-	-	-	3	
	F	-	-	-	-	-	-	3	
	M	-	-	-	-	-	-	2	

each species sex class at the different elevations. In general, the relative abundance of individuals belonging to these three sex-categories (e.g., adult males and females, and juveniles) increased from the higher to the lower elevations. In the discussion, special emphasis will not be given to the observed differences in sex ratios within individual species from elevation to elevation, since this specific issue lies beyond the scope of the present work.

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

First, although at station 4, the Anolis relative abundance was lower (49) than at station 3 (59), the lizard relative density doubled in number at station 4 since here 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 now is a secondary succession, while the Mangle Blanco forest is a climax habitat in pulse stability (Odum, 1971).

Second, the total surface availability was markedly 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 4×10^{-2} lizards/m²) to the Roble Blanco and White Mangrove forests (stations 3 and 4 with 7×10^{-2} and 8×10^{-2} lizards/m², respectively).

Third, the surface area of the trunks is of particular importance to A. gundlachi, A. evermanni, A. stratulus, and A. cristatellus.

Table 7. Perch availability in each of the four study sites expressed in terms of m^2 of surface: area of ground - tree basal area = available ground area, + 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
=	448.26	447.07	448.45	449.21
+	319.95	544.87	452.84	169.27
=	768.21	991.94	901.29	618.48

Table 6. Lizard density expressed in terms of Anolis relative abundance per: 1) tree, 2) m^2 of topographical area, 3) m^2 of tree surface, and 4) m^2 of total available surface (ground and tree). Values are $\times 10^{-2}$.

STATIONS				
	1	2	3	4
1	27	53	47	94
2	7	10	13	11
3	10	8	13	29
4	4	4	7	8

During the day these species mostly utilized trunks.

As a result, trunk surface area was correlated with variations in the lizard relative densities at the four study sites. Accordingly, lizard relative density increased in sites where trees were shorter and had smaller diameter (at breast height) and where lizard relative abundances were greater; compare the "+" row (surface area of trunks) in Table 7 with #3 row (relative abundance/m² 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, 1330-1445 Hrs. on 15 Dec., 1976; at station 3, 1315-1450 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

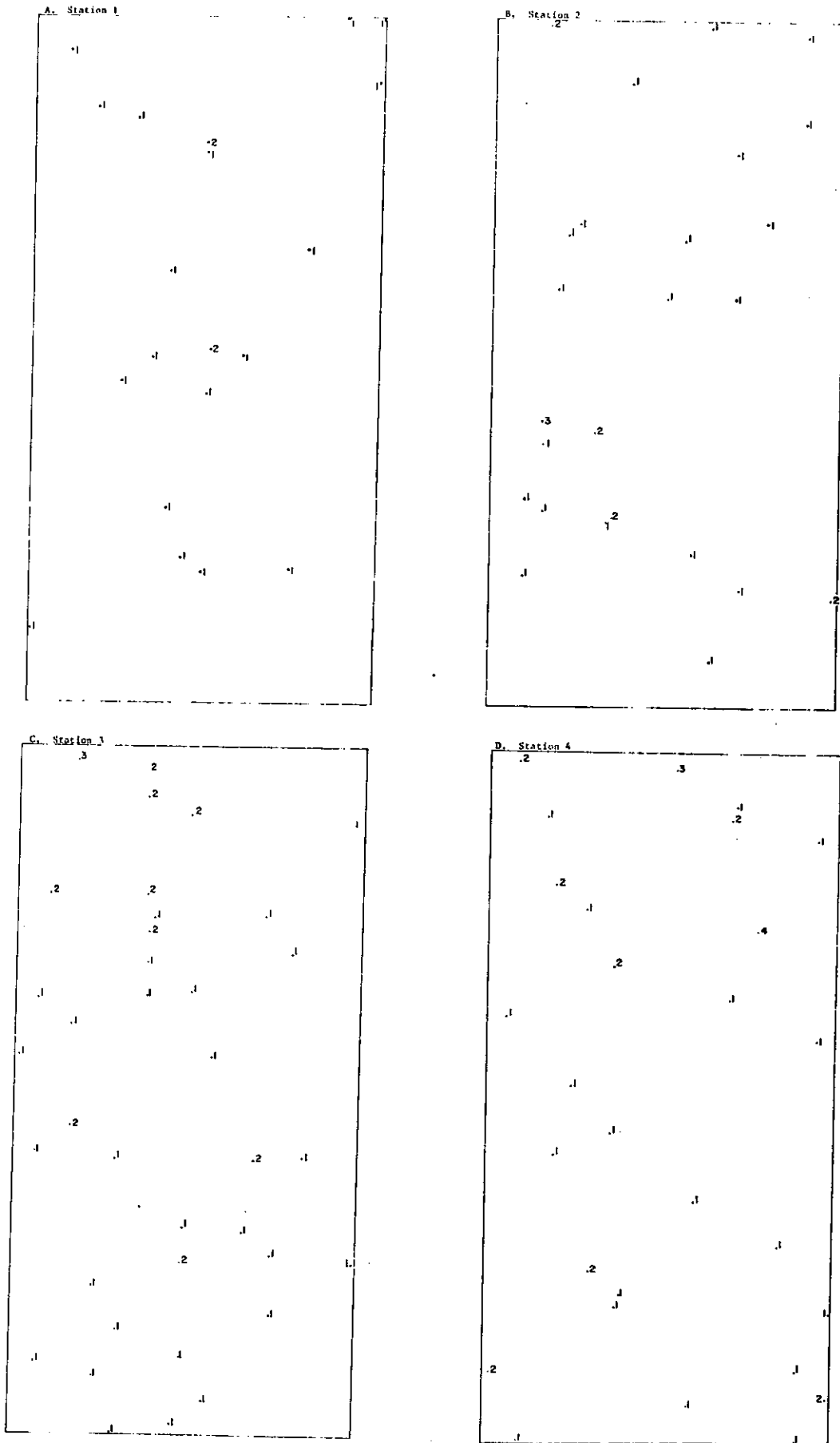


Fig. 9. The lizard spatial distribution during a period of high diurnal activity at stations 1(A), 2(B), 3(C), and 4(D).

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 availability of surface area, and 3) a greater local food availability within the microhabitats. The trees at the SE and W, with 2 and 3 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 3 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 6% 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 (10% of 39): 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 increasing resource availability or with the higher and higher anoline relative density.

Structural Habitat Selection

Table 8 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 respectively show the perch heights and perch diameters chosen by the different Anolis species.

On the basis of structural habitat, we are able to 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 cms) 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+ cms) diameters.

Anolis evermanni juveniles were observed more frequently at perch

Table 8. The different combinations of perch height and perch diameter utilized by the Anolis species sex/size classes (juveniles, females, and males) at each station. The combinations are given in percents of the total of individuals belonging to each one of the species' classes. These totals appear to the left of the sex-class categories.

A. BUDISIBI		STATION 1	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)
1-1 JUVENILES	3.8 FEMALE	4.3 JUVENILES	12.2 FEMALE
218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground
21	1.7	23	09 23 08
22-3	1.7 8.6 1.7	22-3	4.9 11.5 18 08
1-2	7.7 7.7 4.8 7.7 7.7	1-2	6.7 8.9 13.3 4.4 11.1
cl	13.6	cl	13.3 11.1 13.3
ground	7.7	ground	4.4 13.3
			2.5
			88 14.7 59
			118 17.6 29
			2.9
			2.5

A. BUDISIBI		STATION 2	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)
1-1 JUVENILES	7.7 FEMALE	12 JUVENILES	3.3 FEMALE
218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground	218 18-28 8-22 2-1 cl ground
23	10.3 17.3	23	13 31
22-3	14.3 14.3	22-3	7.7 4.6 10.9
1-2	10.7 10.7 3.3	1-2	10.7 10.7 10.7 8.3
cl	3.3	cl	8.3 8.3
ground	3.3	ground	4.6 13.3
			10.7
			4.6
			103 128 77
			77 81 26
			398 77 10.3
			26 26 5.1
			2.6

Table 8. (cont.)

A. stralivius		STATION 2	
PERCH	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	STATION 2
HEIGHT (METERS)	JUVENILES	JUVENILES	MALES
	218 16-28 8-22 2-1 <1 ground	58 FEMALES	218 16-28 8-22 2-1 <1 ground
>3	81 38 45	65 65 32	
>3	91 91	76 43 167 15	129 129 32
2	136 409 182	167 106 108 15	194 97 32
<1	45	76 30 81	97 97 32
ground	45		

A. stralivius		STATION 1	
PERCH	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	STATION 1
HEIGHT (METERS)	JUVENILES	JUVENILES	MALES
	218 16-28 8-22 2-1 <1 ground	5 FEMALES	218 16-28 8-22 2-1 <1 ground
>3	187	400 400 200	333 333
>3	187		
1-2	167 333		333
<1	187		
ground			

A. stralivius		STATION 2	
PERCH	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	STATION 2
HEIGHT (METERS)	JUVENILES	JUVENILES	MALES
	218 16-28 8-22 2-1 <1 ground	5 FEMALES	218 16-28 8-22 2-1 <1 ground
>3			
>2-3			
1-2	100.0		
<1			
ground			

A. stralivius		STATION 2	
PERCH	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	STATION 2
HEIGHT (METERS)	JUVENILES	JUVENILES	MALES
	218 16-28 8-22 2-1 <1 ground	5 FEMALES	218 16-28 8-22 2-1 <1 ground
>3			
>2-3			
1-2	300 800		
<1			
ground			

Table 8. (cont.)

A. cristatellus		STATION 4	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	4 JUVENILES	33 MALES
		>16.16-28 8-22 2-1 <1 ground	>16.16-28 8-22 2-1 <1 ground
>3	4.3 2.2 2.2 2.2		21.2 6.1 9.1
22-3	4.3 10.8 10.8		19.1 6.1 13.0
1-2	17.4 4.3 18.6 4.3		12.1 6.1 9.1
<1	25.0 25.0 25.0 8.5 8.5		12.1 3.0
ground	25.0	4.3	3.0

A. cristatellus		STATION 3	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	3 FEMALES	0 MALES
		>16.16-28 8-22 2-1 <1 ground	>16.16-28 8-22 2-1 <1 ground
>3			
22-3			
1-2	50.0 25.0	333	
<1	25.0	333	
ground		333	

A. cristatellus		STATION 3	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	3 JUVENILES	2 MALES
		>16.16-28 8-22 2-1 <1 ground	>16.16-28 8-22 2-1 <1 ground
>3			
22-3			
1-2	20.0	11.1 11.1	80.0
<1		11.1	90.0
ground	80.0	11.1	94.4

A. cristatellus		STATION 3	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	12 FEMALES	2 MALES
		>16.16-28 8-22 2-1 <1 ground	>16.16-28 8-22 2-1 <1 ground
>3	8.3 8.3 8.3		50.0
22-3	333 8.3		
1-2	50.0 50.0	8.3 16.7 8.3	
<1			50.0
ground			

Table 8. (cont.)

A. stricklandii		STATION 4	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)
2 JULY 1962	2 JULY 1962	8 FEMALES	3 MALES
>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground
>3			400
>2-3			
1-2	16.7	200	200
<1	16.7		
ground	100.0	66.7	200

A. stricklandii		STATION 4	
PERCH HEIGHT (METERS)	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)	PERCH DIAMETER (CENTIMETERS)
2 JULY 1962	2 JULY 1962	11 FEMALES	24 MALES
>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground	>16.16-28.8-22.2-1 <1 ground
>3	50.0	18.3	28.0
>2-3			4.2
1-2	50.0	9.1	12.5
<1		18.2	8.3
ground			8.3

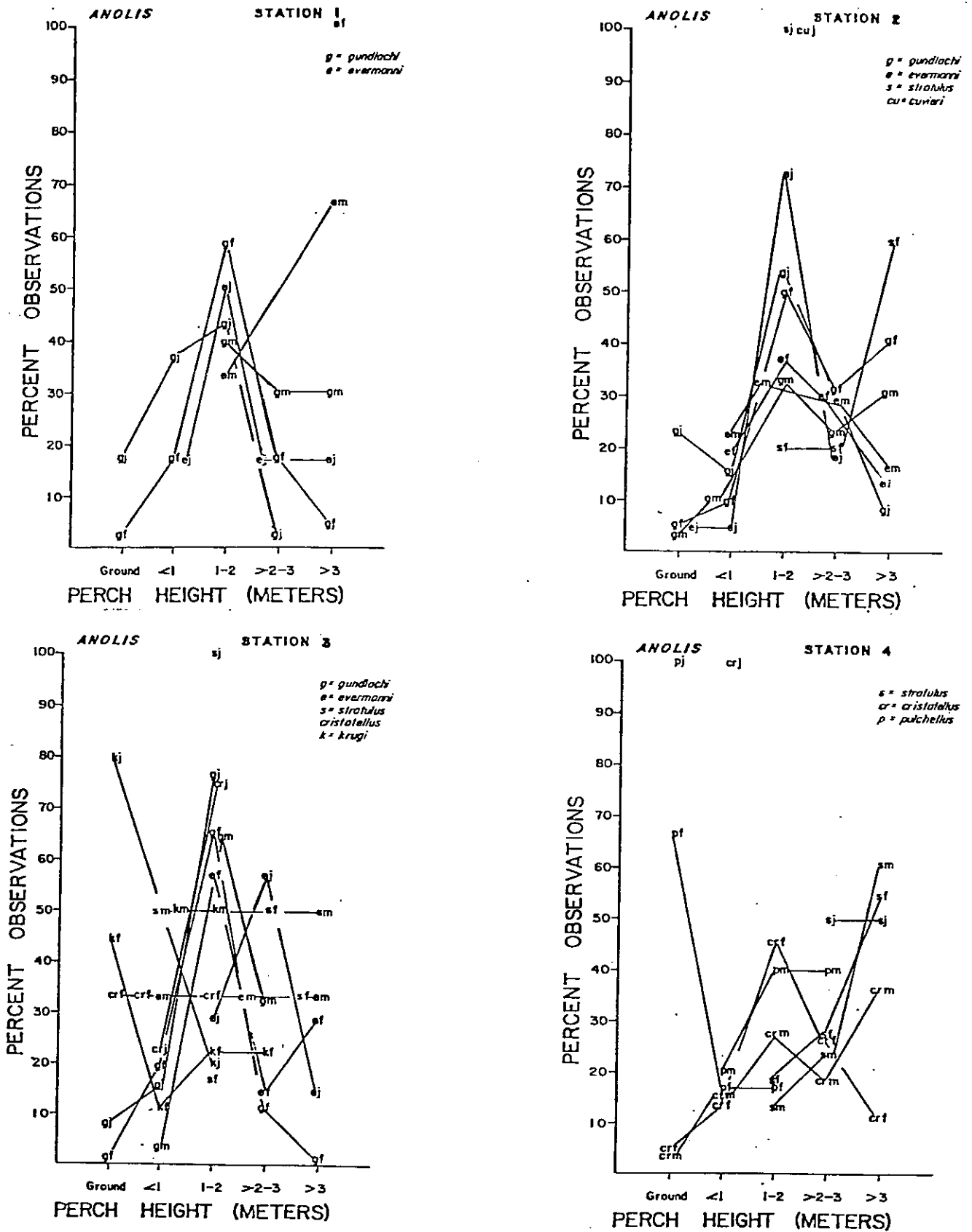


Fig. 10. The percent of observations of the *Anolis* perch height distributions at each of the forest habitats. Percentage is of total for each sex class/species over range of perches. The symbols j, f, m indicate juveniles, females, and males, respectively.

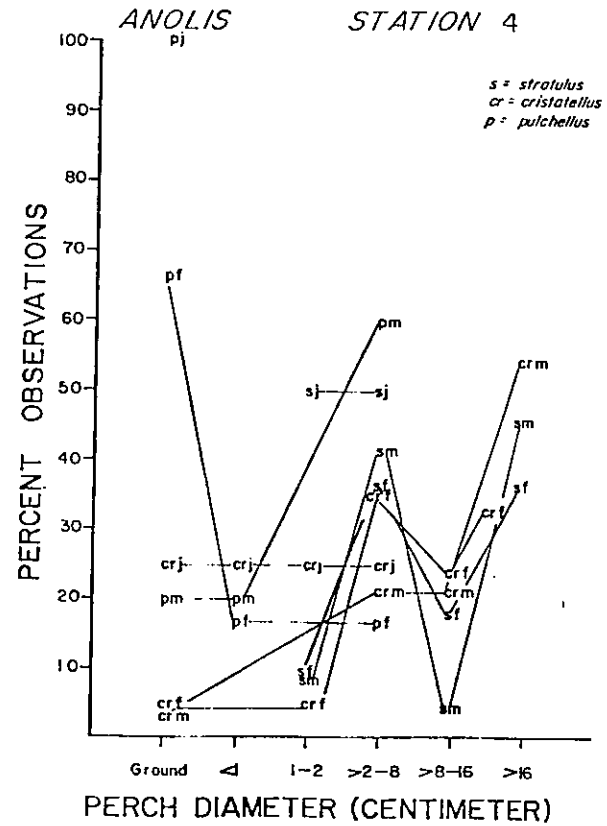
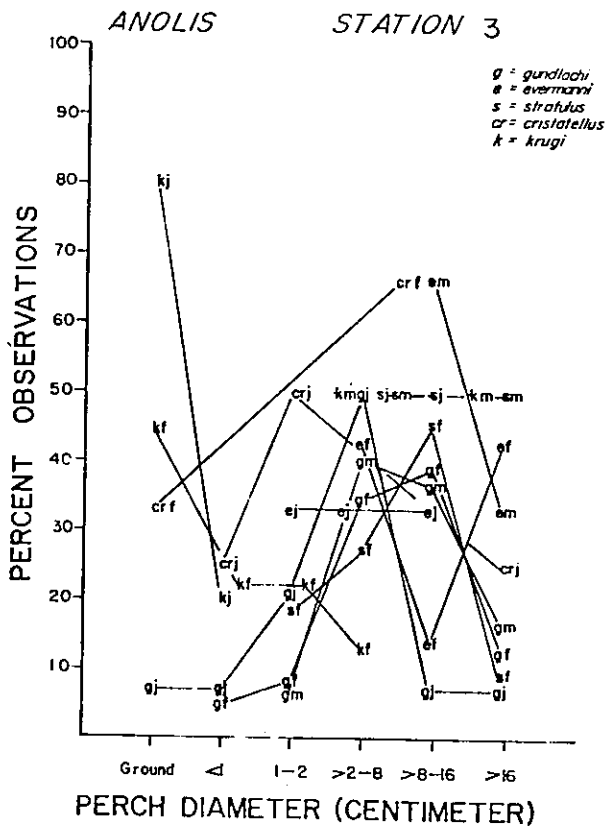
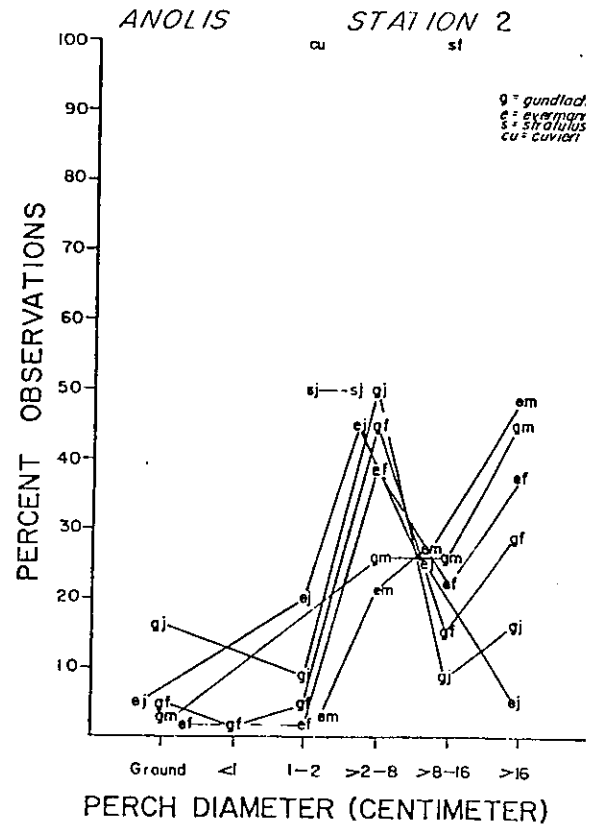
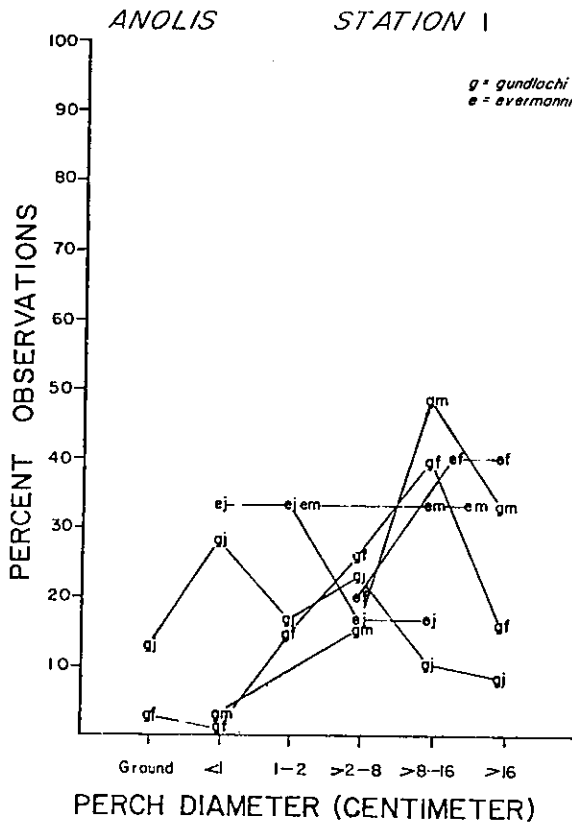


Fig. 11. The percent of observations of each Anolis species at every study site showing the utilized perch diameters.

heights of 1 to 3 meters on perch diameters of less than one centimeter to sixteen at the first three sites where they occurred; all but the mangrove forest site. A. evermanni females were found on high perches at 1 to more than 3 m and of small to large (2 to more than 16 cms) sizes. At the Sierra palm brake (station 1), A. evermanni males were observed only three times: at 2 m and at more than 3 m 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 m and on moderate to large diameters of 8 to more than 16 cms. 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 m at stations 2 and 3, but at station 4 they climbed higher up to more than 3 m on the small to moderate (1-8 cms) perches. These juveniles, at sites 2 and 3, were observed on perch diameters of 1 to 8 cms and 2 to 16 cms, 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 cms), 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 cms small perch at 2 m high.

Anolis cristatellus juveniles occurred fairly close to ground at stations 3 and 4, and up to 2 m on very small (< 1 cm) to moderate (8 cms) perches. The females were found close to 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 perched either very high at more than

3 m (similar to A. stratulus, A. gundlachi, and A. evermanni males at their respective sites), or fairly close to the ground at less than 1 m similar to A. evermanni males at station 2.

Anolis krugi juveniles, found at station 3, occurred in the understory ground vegetation of the site and climbed up to 1 m high on small saplings and seedlings of less than 1 cm wide. The females perched higher than the latter and utilized small to moderate (1 to 8 cms) 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 his congeners. The juveniles were only found on the ground, the females on the ground and at 2 m high, and the males also on the ground and at 3 m 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 the result of these variations, different species were found at the altitudinal extremes and were classified in 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. Again,

Table 9. The microclimates of the Anolis species found at the four forest habitats shown in percents. The numbers in parenthesis are the total observations for each species at the given site.

<u>ANOLIS CLIMATIC HABITAT IN %</u>				
SPECIES	STATIONS			
	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>
	<u>sun s/sd shade</u>	<u>sun s/sdshade</u>	<u>sun s/sd shade</u>	<u>sun s/sd shade</u>
<u>gundlachi</u>	7.2 (125)	10.4 82.4 (92)	9.8 9.8 80.4 (88)	3.4 21.6 75.0
<u>evermanni</u>	83.3 (6)	16.7 24.7 18.5 56.8 (81)	6.7 53.3 40.0 (15)	
<u>stratulus</u>		16.7 50.0 33.3 38.5 15.4 46.2 (6)	61.1 5.6 33.3 (36)	
<u>cuvieri</u>		100.0 (1)		
<u>crisatellus</u>		33.3 (3)	66.7 (50)	74.0 4.0 22.0
<u>krugi</u>		25.0 37.5 37.5 (8)		
<u>pulchellus</u>				84.6 15.4 (13)

a highland species sun-adapted at a high elevation habitat, has 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. As 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 33%, 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 mm) and more frequent prey

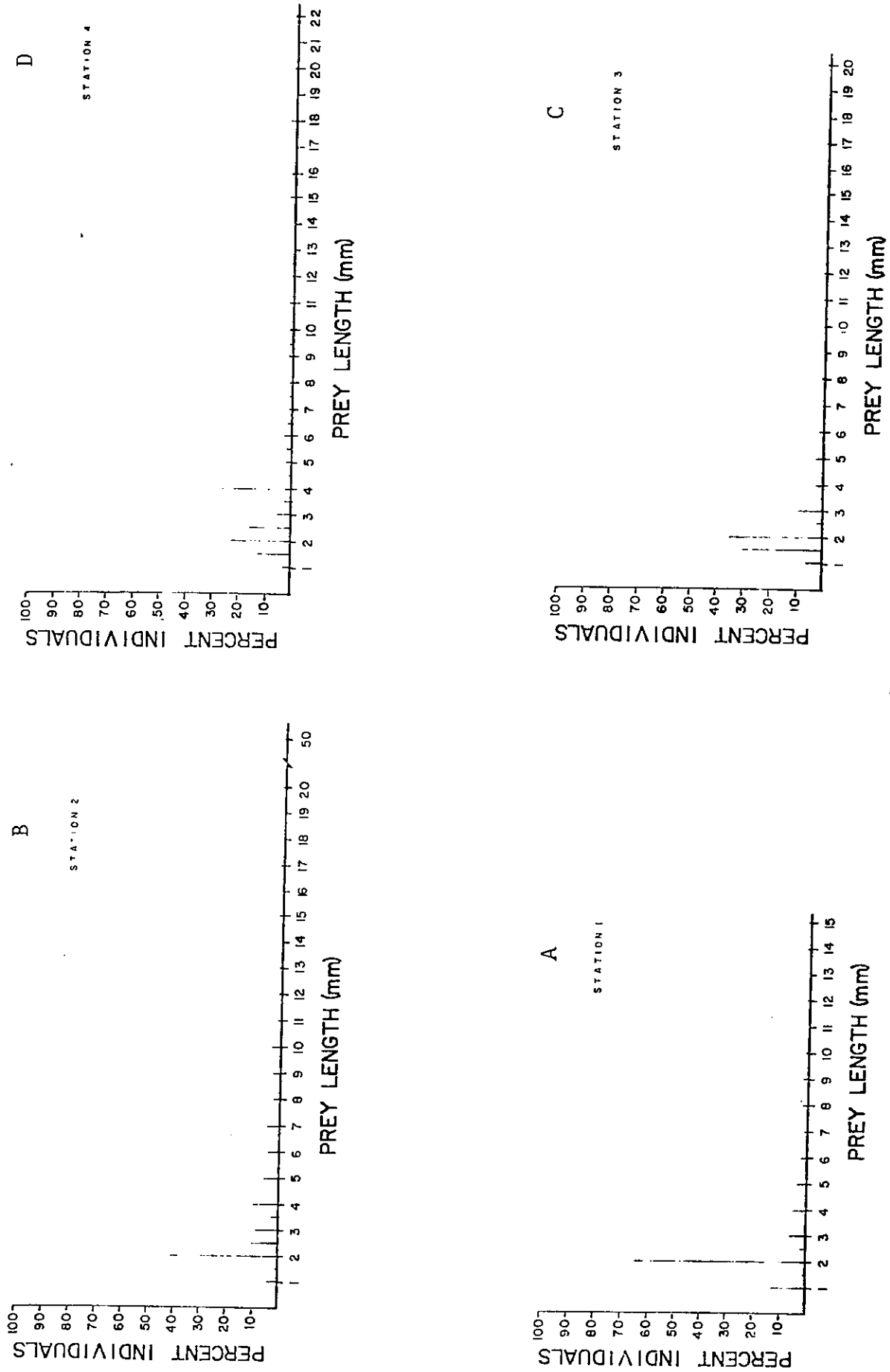


Fig. 12. The percent relative frequency distribution of the prey lengths found in the stomach contents of all the Anolis lizards captured. A. The distribution at station 1; B. The distribution at station 2; C. The distribution at station 3; D. The distribution at station 4.

sizes. At station 4, the prey size of higher relative frequency was 4 mm. 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 Anolis, as well as over 75% females, and the large size-class included only the adult males of several species.

At station 1 (Fig. 14-A), the small size-class category (16% of 31 lizards) included lizards belonging to the 20-35 mm size interval. Their mean prey length was 2.11 mm (SD = 0.20 mm). The intermediate category (58% of 31 lizards) included sizes of 35-50 mm snout- vent length, and their mean prey length was 2.81 mm (SD = 0.60 mm). The maximum ranges

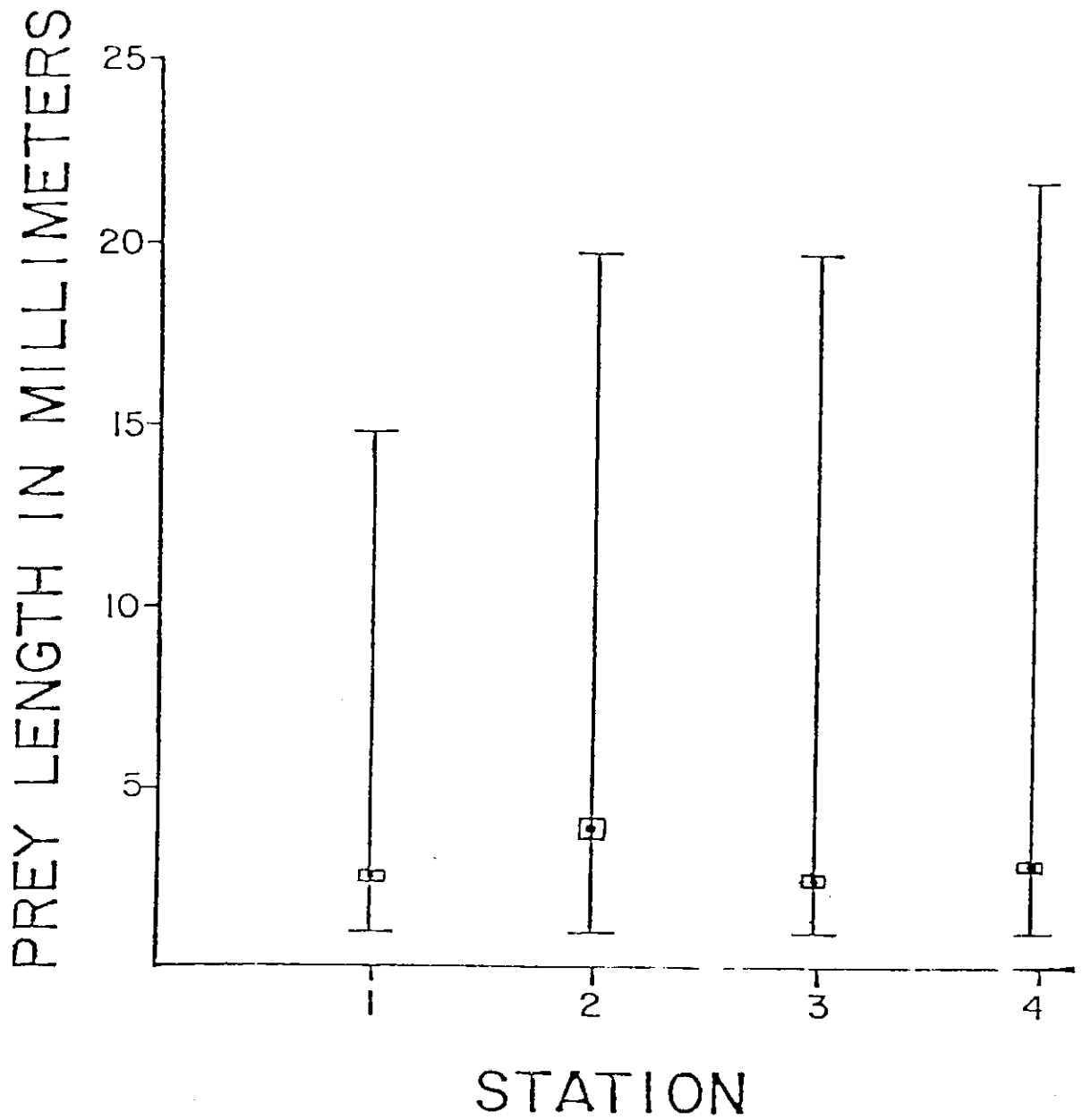


Fig. 13. The mean of prey lengths eaten by all individuals sampled at each of the four study sites. The standard error of the means is shown by the rectangles, and the ranges by the bars.

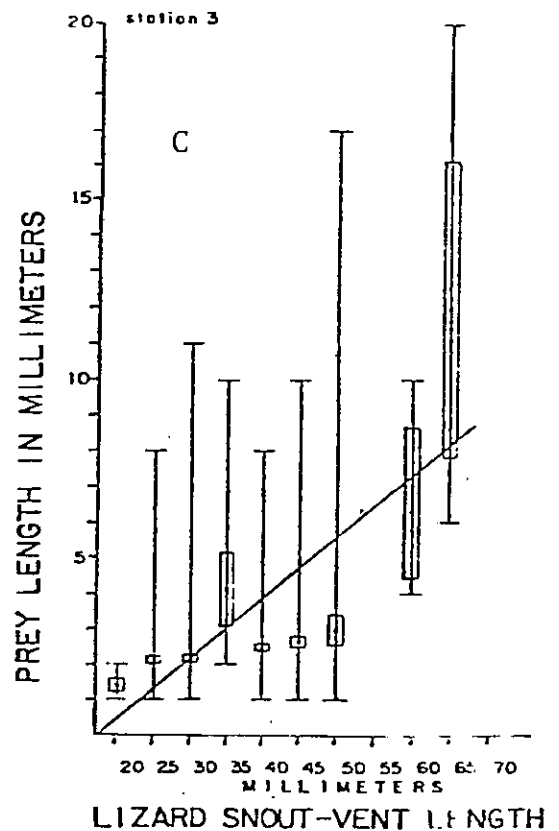
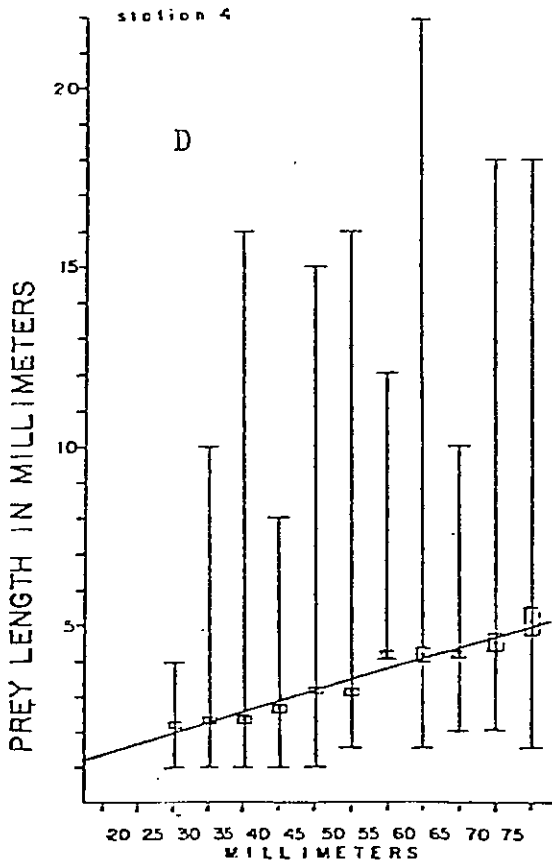
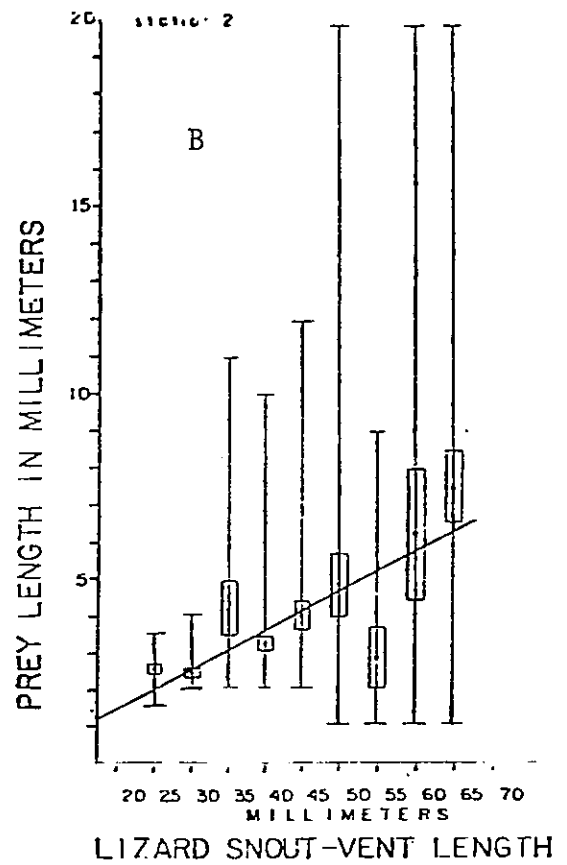
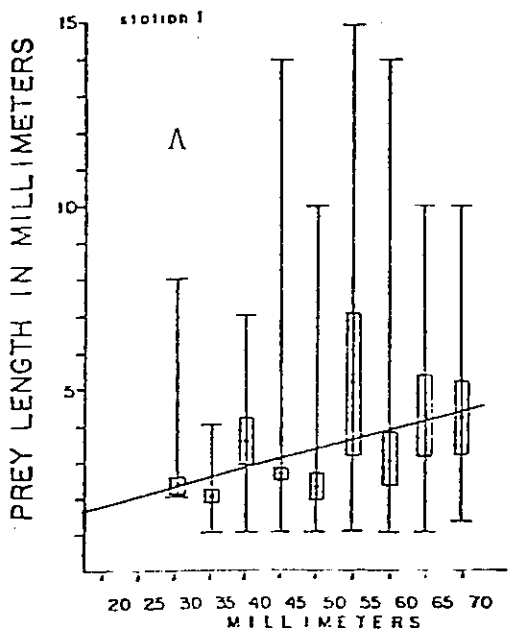


Fig. 14. The means of prey lengths eaten by the different sizes of lizards sampled at each study site. The rectangles show the standard error of the means, and the bars the ranges. Regression lines of the prey length means are shown for each of the stations. See Table 10 for the sample size of each lizard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

Table 10. The percentages of the species sex-classes belonging to the snout-vent length class intervals at each one of the study stations: E, G, S, Cr, K, P, stand for each of the species collected for stomach contents analysis as in Table 9; J, F, M, represent the sexes. The asterisks are young adult males.

S-V Lengths (mm)	Stations			
	1	2	3	4
16-20	-	-	N=1 100 CrJ	-
20-25	N=1 100 GJ	N=2 100 GJ	N=13 77 GJ 33 KJ	-
25-30	N=2 100 GF	N=4 50 GJ 25 SJ 25 EJ	N=10 50 GJ 10 CrJ 10 CrF 10 EJ 10 KF 10 CrM*	N=4 25 CrJ 25 SJ 25 PF 25 PM*
30-35	N=2 50 GF 50 GJ	N=3 66 EF 34 GF	N=2 50 GJ 50 CrF	N=4 25 CrJ 25 SM* 25 PF 25 PM*
35-40	N=2 50 GF 50 EF	N=7 43 GF 57 EF	N=6 50 GF 17 EF 17 SF 17 GM*	N=6 33 CrM* 33 SF 33 SM
40-45	N=12 100 GF	N=5 100 GF	N=8 63 GF 13 GM* 13 CrF 13 SM	N=4 75 CrF 25 CrM*
45-50	N=4 50 GF 25 EF 25 GM*	N=5 20 GF 40 EF 40 GM*	N=3 33 GF 67 GM*	N=10 40 CrF 10 SF 30 SM 20 PM
50-55	N=1 100 GM*	N=1 100 GM*	-	N=4 25 CrF 50 CrM* 25 SM
55-60	N=2 50 GM 50 EM	N=3 66 EM 34 GM	N=1 100 GM	N=1 100 CrM*
60-65	N=2 100 GM	N=4 75 GM 25 EM	N=1 100 GM	N=3 100 CrM
65-70	N=3 100 GM	-	-	N=4 100 CrM
70-75	-	-	-	N=2 100 CrM
75-80	-	-	-	N=6 100 CrM

Table 11. Mean sizes in millimeters and 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.

MEAN-SIZE VARIATION OF LIZARD SIZE & SEX UPPER CLASS INTERVALS

SPECIES	SEX	STATIONS						
		1	2	3	4	5	6	
G	J	34.25	-21.17	27.00	18.52	32.00	-	-
	F	46.50	- 1.08	46.00	2.17	47.00	-	-
	M	69.00	-10.15	62.00	4.84	65.00	-	-
E	J	-	-	35.00	-17.14	29.00	-	-
	F	48.00	4.17	50.00	-22.00	39.00	-	-
	M	60.00	5.00	63.00	-	-	-	-
S	J	-	-	28.00	- 7.14	-	-	26.00
	F	-	-	-	-	39.00	20.51	47.00
	M	-	-	-	-	45.00	18.89	53.00
Cu	J	-	-	43.70	-	-	-	-
	F	-	-	-	-	-	-	-
	M	-	-	-	-	-	-	-
K	J	-	-	-	-	22.67	-	-
	F	-	-	-	-	30.00	-	-
	M	-	-	-	-	-	-	-
Cr	J	-	-	-	-	27.00	14.82	31.00
	F	-	-	-	-	41.00	26.83	52.00
	M	-	-	-	-	-	-	78.17
P	J	-	-	-	-	-	-	28.50
	F	-	-	-	-	-	-	33.00
	M	-	-	-	-	-	-	48.75

of prey items taken by the small, intermediate, and large lizards were 8, 14, and 15 mm, respectively. The large adults (50-70 mm) ate a mean prey length of 4.16 mm (SD = 0.87).

At station 2 (Figure 14-B), the small lizards (18% of 33 lizards) with snout-vent length of 20-30 mm ate prey with a mean length of 2.51 mm (SD = 0.10 mm). The intermediate lizards (58% of 33) with 30-50 mm s-v length took 4.06 mm mean prey length (SD = 0.67 mm). The large representatives (24% of 33) were 50-65 mm and ate 5.59 mm mean prey length (SD = 2.52 mm). The maximum ranges of prey items taken by the small, intermediate, and large representatives were 4, 20, and 20 mm, respectively.

At station 3 (Figure 14 - C), the small lizards (53% of 45 lizards) with snout-vent length of 16-30 mm ate prey with a mean length of 1.89 mm (SD = 0.43 mm); the intermediate lizards (43% of 45) with 30-50 mm took prey with a mean length of 3.06 mm (SD = 0.74 mm); and the large lizards (4% of 45) with 50-65 mm snout-vent length ate prey with a mean length of 9.17 mm (SD = 4.01 mm). The maximum ranges of the small, intermediate, and large lizards were, respectively, 11, 17 and 20 mm.

At station 4 (Figure 14 - D), the small lizards (8% of 48 lizards) with s-v length of 25-30 mm ate prey with a mean length of 2.22 mm (SD = 0.63 mm); the intermediate lizards (50% of 48) with 30-50 mm s-v length ate prey with a mean length of 2.62 mm (SD = 0.37 mm); and the large lizards (42% of 48) with 50-80 mm s-v length took a 4.19 mm (SD = 0.64 mm) mean prey length. The maximum ranges of the small, intermediate, and large lizards were respectively, 4, 16 and 22 mm.

At the 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 also appear the regression curves of the means of prey lengths eaten by Anolis of different snout-vent lengths at each of the four study sites. This analysis produced the following coefficients of determination: .4560 for station 1, .6185 for station 2, .6426 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. The same way, 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 preys are displayed in Figure 16. The cumulative frequency distribution of these potential-prey sizes found at each of the four habitats appear 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

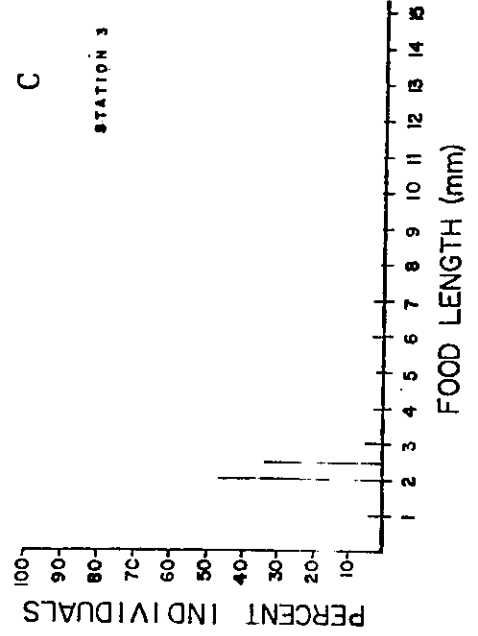
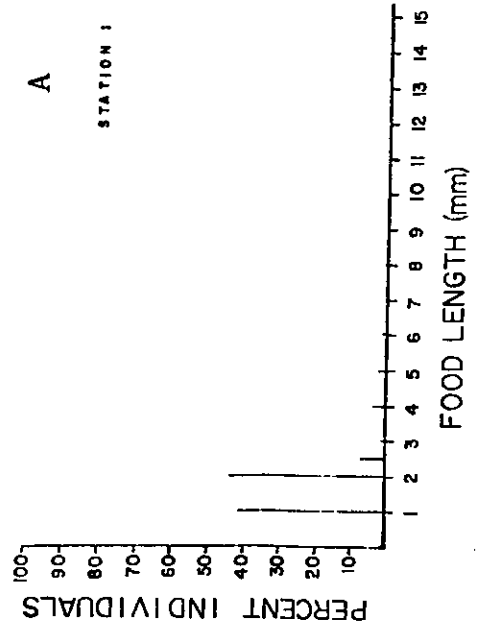
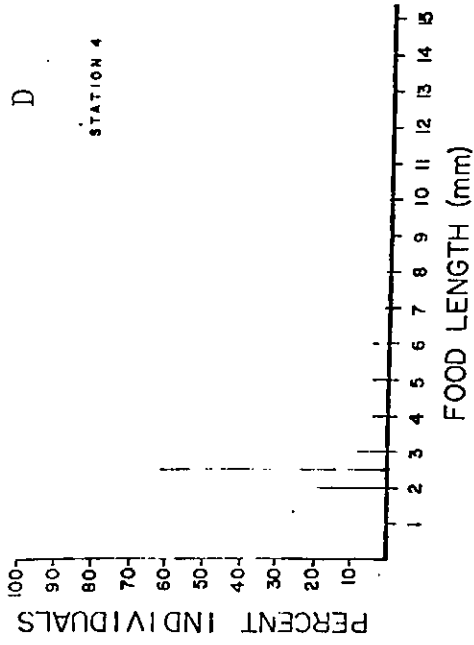
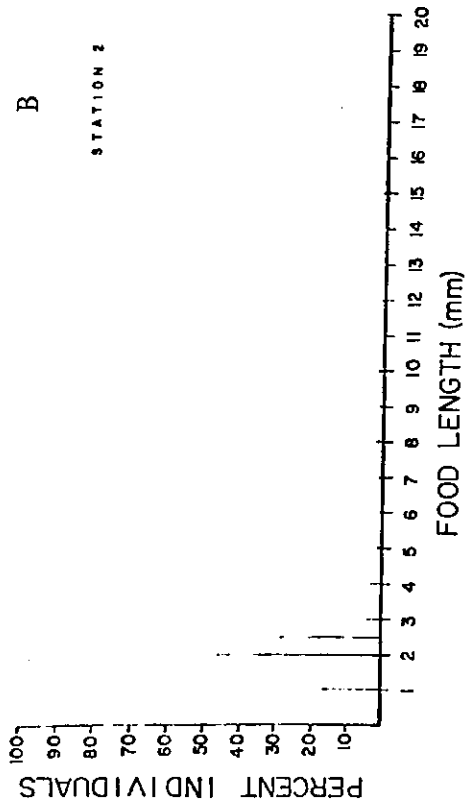


Fig. 15. The percent relative frequency distributions of the potential-prey lengths sampled at the four study sites.

frequency distributions of the food available to the Anolis species. 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 3 mm. Nevertheless, stations 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 3 was 2.67 mm, and 2.67 mm at station 4. The calculated coefficients of variation ($S/\bar{x} \times 100$) were, in respective order, 54.0, 23.3, 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

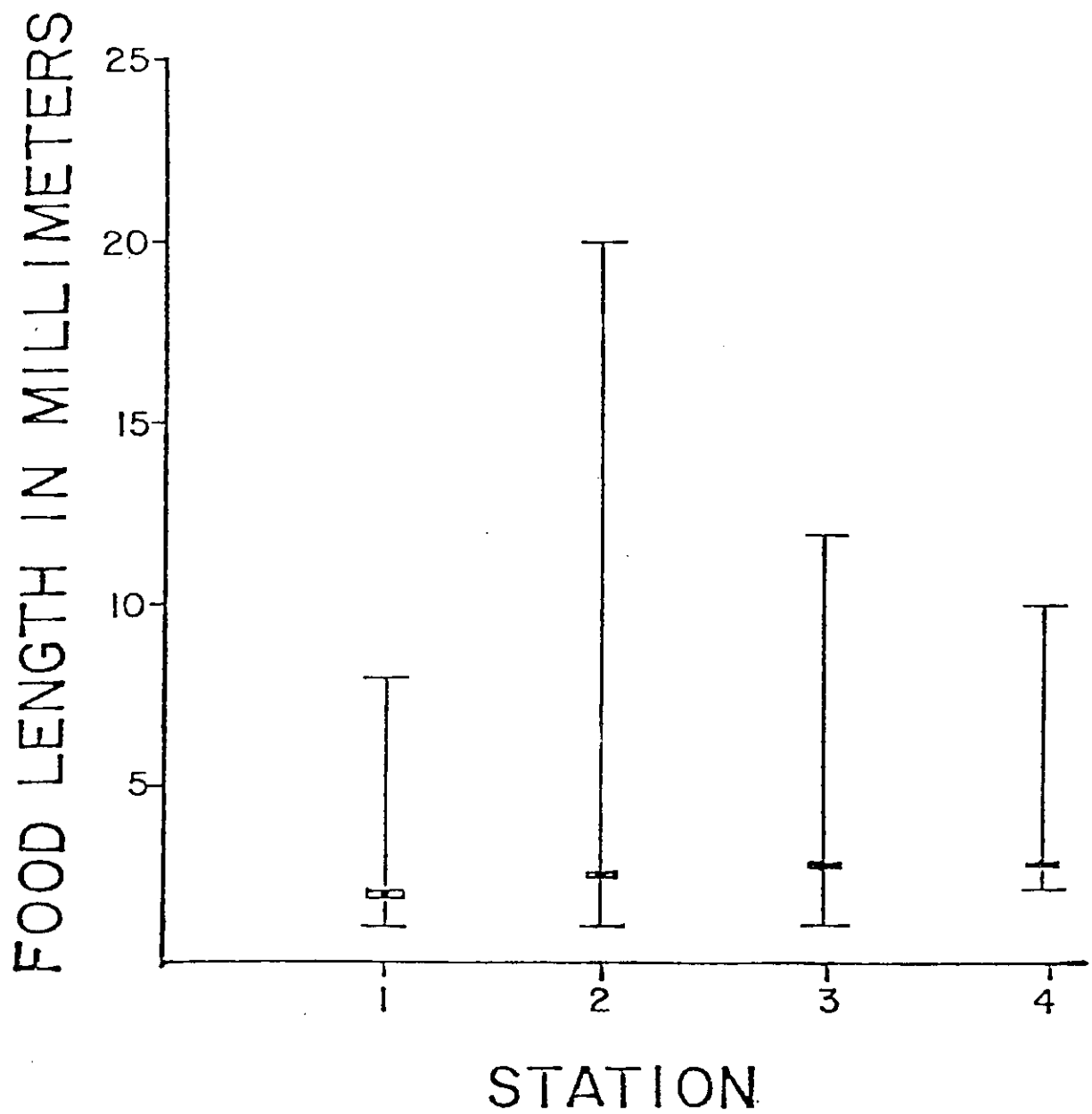


Fig. 16. The means of food lengths sampled at each of the four study sites. The standard error of the means is shown by the rectangles, and the ranges by the bars.

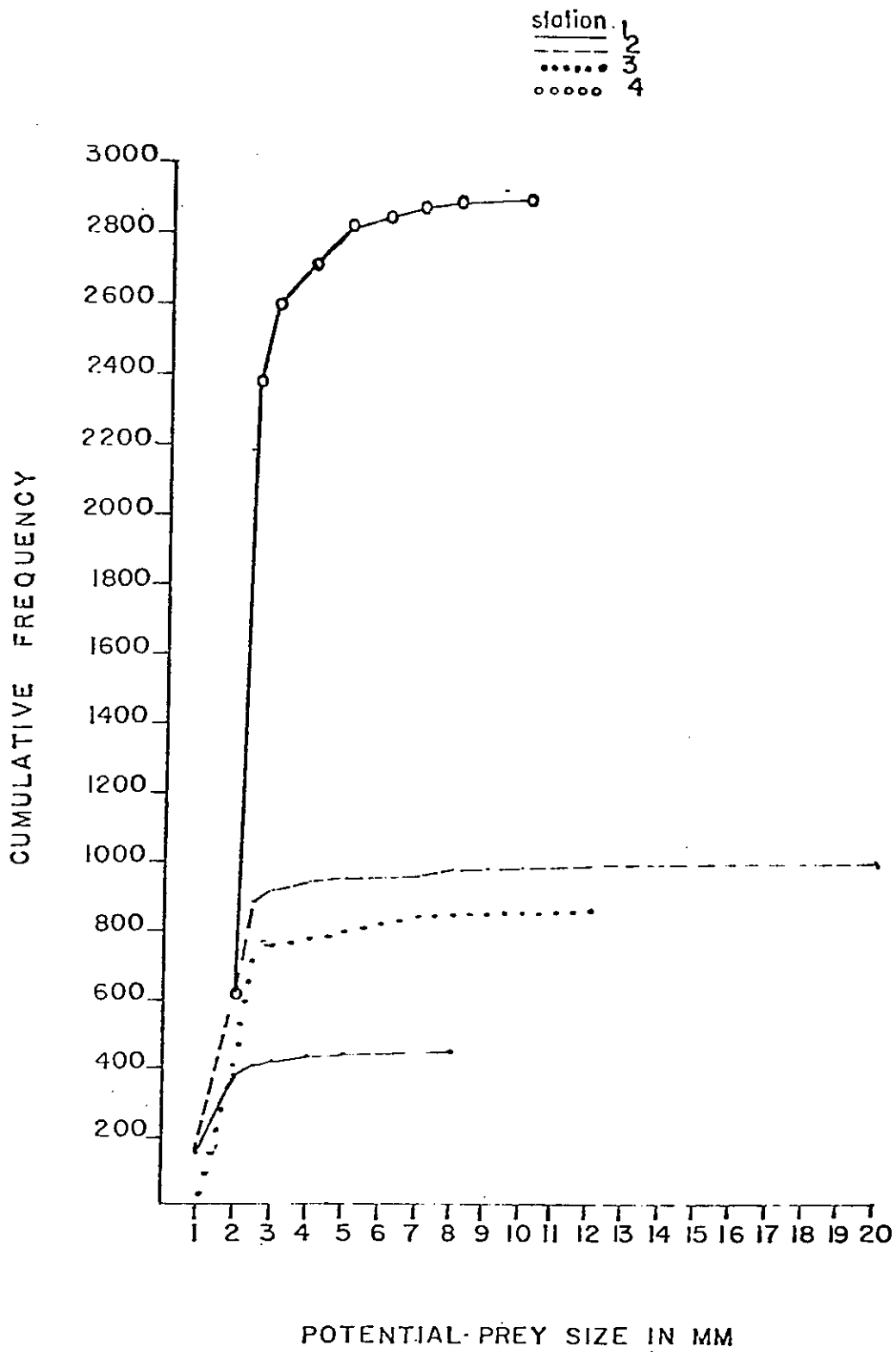


Fig. 17. The cumulative frequency distributions of the potential-prey lengths sampled at the four study sites.

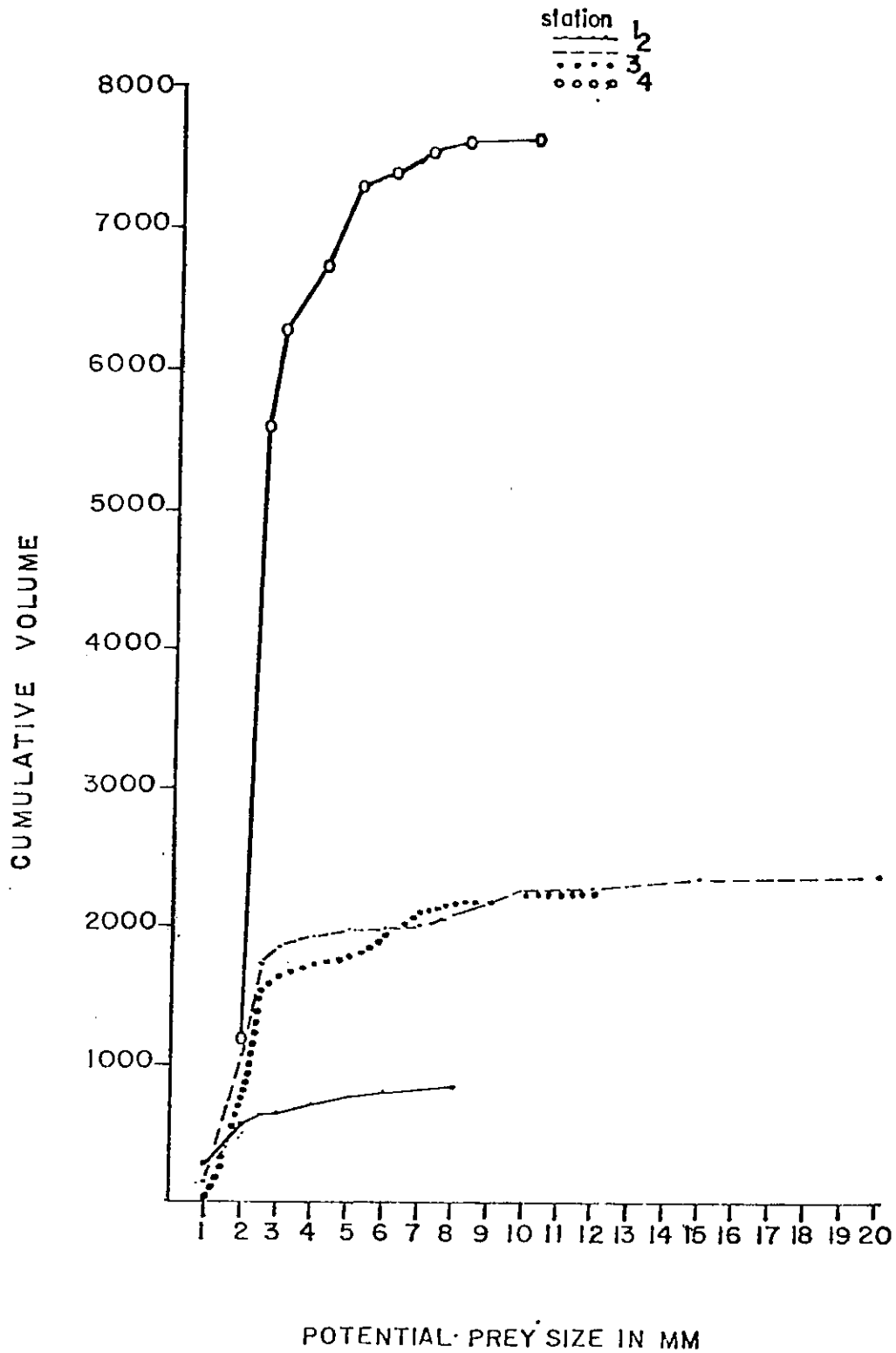


Fig. 18. The cumulative volume distributions of the potential-prey lengths sampled at four study sites.

a cumulative pattern similar to that of the cumulative frequency. These volumes were estimated at all the stations: station 1 with 807 mm³, 2 with 2381, 3 with 2281, and station 4 with 7681 mm³. At the intermediate stations 2 and 3, 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 a 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 23.79°C 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 and every elevation. The standard errors of the means for stations 1 and 2 were 0.98 and 0.76°C, respectively. These yield low coefficients of variations of 5% and 3%, respectively. These coefficients suggest that both sites show slight and similar variations in temperature.

The mean 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,

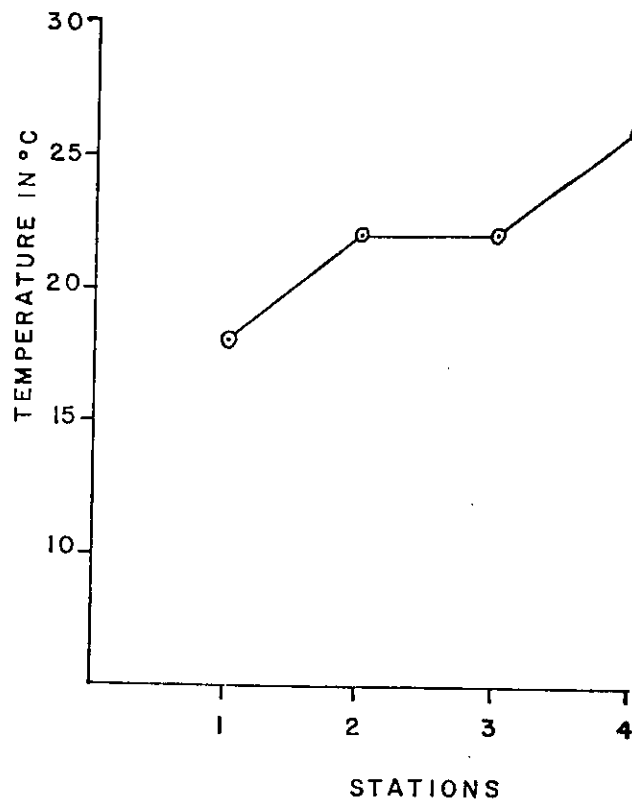
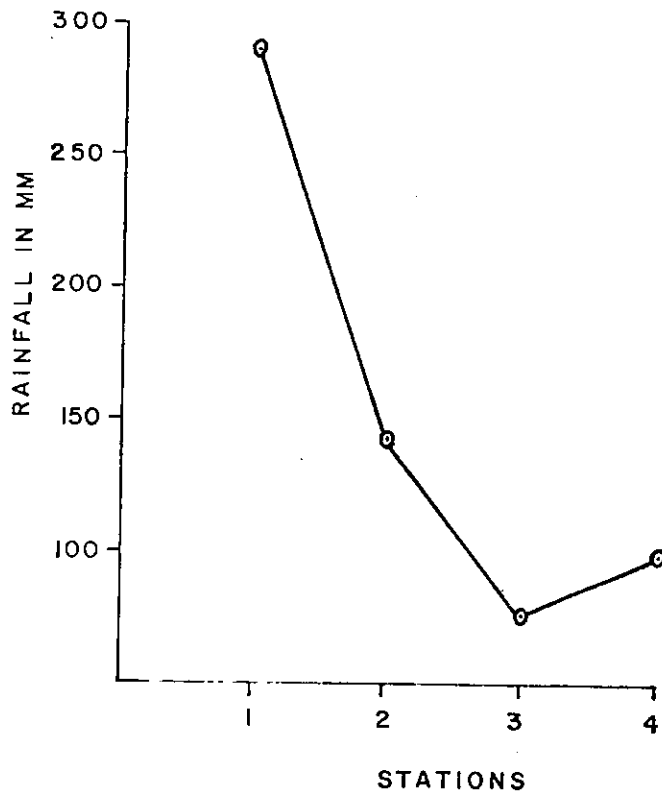


Fig. 19. The climatic data averaged for the temperature and rainfall recorded during the period from November to February of the three previous consecutive years; from Nov. 1974 to Feb. 1977.

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 39.12 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 are shown the diversity indexes of the lizard and tree species found at each of the forest habitats. The observed patterns indicate that as the tree index increased, the lizard index also increased except at the mangrove forest site that 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 habitat regardless of the tree species diversity. The tree composition and age of every habitat could have a cause-and effect relation with the availability of surface areas and the number of microclimates available to these lizards.

Number and Area of Microhabitats

In Table 13-A appears 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 species found at the 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	2.14	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 m².

A. Structural Microhabitat	Stations			
	1	2	3	4
Trunk	320	545	453	169
Understory Vegetation	369	-	351	198
Leaf and Wood Litter	81	447	99	252
B. Climatic Microhabitat				
Shady, Closed Canopy	-	414	99	-
Intermediate, Semiclosed Canopy	342	36	306	54
Sunny, Semiopened Canopy	108		45	396

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, at stations 1 and 3 occurred the larger understory vegetation areas.

At station 4, the mangrove seedlings of about 10 cms high were included within the leaf and wood litter category, since these were not found intermingled with grasses or saplings of more than 30 cms. high. At station 1, the understory vegetation cover was composed, among other plants, of ferns, mosses and liverworts, bromeliads, very short Sierra palms (Prestoea montana), and Camasey species. 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 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 13-B indicate the existence of a number of different climatic regimes 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 shade, while the lowland species A. cristatellus (i.e., its morphological counterpart) was found in the sun with remarkable 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 Río Espíritu 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 8, Figure 10 and 11); the available surface area of the different structural microhabitats (Tables 7 and 13); 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 study documents that at sites with greater food relative abundance (i.e., lowlands), the lizard relative abundance and density were greater too. Furthermore, the relative densities of the individual species seem more difficult to interpret than the total density of the entire community, since the variation in the number of individuals of a given species from one elevation to the next may, indeed, be determined by many more limiting factors (i.e., climatic,

microclimatic, structural, behavioral-territorial, interspecific interactions as well as intraspecific, food availability, predators), while the total number of individuals regardless of species would, in the final analysis, be determined by the community. Thus, the variation in the lizard relative densities along an altitudinal cline suggests that food and structure availability play important roles in the existence of the natural populations of Anolis integrated as a whole. However, water availability may also regulate anoline life histories by causing egg or juvenile mortality as with populations of Anolis acutus on St. Croix, U.S. Virgin Islands (Ruibal and Philibosian, 1974) and Anolis limifrons in Panamá (Sexton, 1967). The study sites of the present paper do not seem to differ significantly from each other in the availability of water or moisture during the wet season to produce a negative effect on eggs laid 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, of 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 Panamá, A. limifrons showed a density of 0.03 lizards/M² (Sexton et. al., 1963; Sexton, 1967). The density of A. nebulosus in Mexico (Jenssen, 1970) was shown to be 0.06-0.09 lizards/ M². Anolis acutus on St. Croix (U.S., V.I.) had 0.43 lizards/M² which is an exceptional population density for the genus (Ruibal and Philibosian, 1974). Anolis pulchellus on Puerto Rico was estimated at 20,000 per hectare (Gorman and Harwood, 1977), or about 2 lizards/M².

Ecological Aspects on 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, relatively hot, wet, and food-rich that would support a relatively higher lizard abundance.

The individuals of most natural populations usually occur in randomly distributed groups or clumps, and in regard to the Anolis of this study, the intermediate-elevation and lowland species appeared in groups of 2, 3, or 4 lizards. The highest number of lizards perching together with other lizards on only some of the trees at a site was observed at station 4, the lowland mangrove habitat. This pattern varied along the cline 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 a 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.
- _____, 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, Río Piedras, Puerto Rico.
- Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern Florida. *Bull. Mus. Comp. Zool.* 125(5): 137-162.
- Dobzhansky, T. and C. Pavan. 1950. Local and seasonal variations in relative frequencies of species of Drosophila in Brazil. *J. Anim. Ecol.* 19:1-14.
- Fitch, H. S. 1972. Ecology of Anolis tropidelopsis in Costa Rican cloud forest. *Herpetologica* 28: 10-21.
- Gorman, G. C. and L. Atkins. 1967. The relationships of Anolis of the roquet species group (Sauria: Iguanidae). II. Comparative chromosome cytology. *Syst. Zool.* 16:137-143.
- _____, 1969. The zoogeography of Lesser Antillean Anolis lizards: an analysis based upon chromosomes and lactic dehydrogenase. *Bull. Museum Comp. Zool.* 138:53-80.
- Gorman, G. C. and R. Harwood. 1977. Notes on population density, vagility, and activity patterns of the Puerto Rican grass lizard, Anolis pulchellus (Reptilia, Lacertilia, Iguanidae). *J. Herp.* 11(3): 363-368.
- Gorman, G. C. and P. L. Licht. 1974. Seasonality in ovarian cycles among tropical Anolis lizards. *Ecology* 55:360-369.
- Gorman, G. C., R. Thomas, and L. Atkins. 1968. Intra- and interspecific chromosome variation in the lizard Anolis cristatellus and its closest relatives. *Breviora Mus. Comp. Zool.* 293: 1-13.
- Jenssen, J. A. 1970. The ethoecology of Anolis nebulosus (Sauria, Iguanidae). *J. Herpetol.* 4:1-38.
- Le Clerg, E., W. H. Leonard, and A. G. Clark. 1962. *Field Plot Technique*. 2nd ed. p.83. Burgess Publishing Company.
- Levins, R. and H. Heatwole. 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. and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean Anolis lizards. *Univ. Calif. Publ. Zool.* 95:1-52.
- _____, 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.* H. T. Odum (Ed.), pp I-8I--I-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 lineatopus *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 Survey 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. II. 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. *Copeia* 1:219-222.
- 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. 1904:551-720.
- 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 zoogeography of anoline lizards on small islands. *Q. Rev. Biol.* 44:345-389.