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TROPICAL RAIN FOREST CYCLING AND TRANSPORT PROGRAM
PHASE I REPORT

Prepared by:

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CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO — U.S. DEPARTMENT OF ENERGY

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1.0 SYNOPSIS

This program was designed to fulfill the clear need for a comprehensive understanding of cycling and transport processes in tropical rain forest ecosystems so that the ecological consequences of energy development can be adequately evaluated. The original program plan (June 1980) has been modified, but the basic approach has not been altered. A primary objective of Phase I was to identify major reservoirs of nutrients and energy within the forest and determine the major pathways of movements among them. Tasks were organized according to the simplest meaningful ecosystem subdivisions (Figure 1). Other relevant aspects of ecosystem organization (e.g. areal homogeneity, seasonality, etc.) were also investigated.

The study area is situated in tabonuco forest within an elevational range of 250-300 m. Average annual rainfall is approximately 3.3 m. Four randomly selected plots (1 ha each) were surveyed and marked within the study area during July 1980. A transect 300 m long was placed diagonally through each plot, and a single 300 X 300 m grid (staked at 30 m intervals) was established during the 1981 wet season.

Calorimetric measurements have been made on plant and animal taxa identified as important components of the ecosystem. Chemical analyses were performed on the same groups in order to determine elemental composition (e.g. calcium, carbon, magnesium, sodium, etc.) and standing crop biomass for each major ecosystem compartment (Figure 1). Preliminary results indicate a general similarity in the proportions of elements and in the caloric content between taxa sampled within the forest and related taxa from other biotic regions.

Litterfall sampling provided information on primary productivity. Leaf fall was used to estimate net primary productivity and was used as the basis for comparing primary productivity during Phase I with four years of similar investigations (1970-73) in the same area. No annual differences were detected among the four sample plots in Phase I, nor were any of the five years significantly different ($p > 0.05$). Highly significant differences were detected among months, however, indicating a marked seasonality in litterfall. The highest leaf litter fall rates occurred at the end of the dry season and beginning of the wet season (March-June).

A value of $1.39 g/m^2$ day was obtained from the combined five years of data. These results are similar to the estimate of $1.43 g/m^2$ day obtained by Wiegert (1970) in his 1965-66 research conducted in the same area as part of the irradiated rain forest program. This consistency in rate of litterfall suggests that the tabonuco rain forest at El Verde is in a functionally mature state. The uniformity in rates among the four 1 ha sample plots indicates that at that scale of measurement the forest is homogenous with respect to primary production.

Identification of major reservoirs and principal pathways of movement of energy and nutrients through the rain forest food web resulted from Phase I field studies and review of the literature. Although numerous investigators have conducted studies on animals within the forest, most authors concentrated on selected groups and selected aspects of trophic interrelationships. Our field efforts, therefore, focused on supplementing published information and determining the interrelationships among the major animal groups.

Many characteristics of food web organization reflect the insular nature of the El Verde forest. In contrast with comparable mainland rain forests, there are no large herbivores, or carnivores (e.g. monkeys, tapirs, jaguars, etc.). The largest common native species are the red-tailed hawk and red-necked pigeon. The Puerto Rican boa is larger (2-3 kg), but is rare within the study area, and probably uncommon throughout the forest (Reagan and Zucca 1982). Introduced species which have become successfully established in the forest (Indian mongoose and roof rat) are also relatively small.

Although smaller in individual size, lizards (Anolis spp.) and arboreal frogs (Eleutherodactylus spp.) are the dominant secondary and tertiary consumers in the forest because of their high population densities. Total lizard densities are greater than 20,000 individuals/ha (see section 5.4.2), and arboreal frog densities within the area exceed 40,000/ha. Despite the relatively slow feeding rates characteristic of cold-blooded animals, the sheer numbers of lizards and frogs makes them more important in the food web at El Verde than in comparable mainland sites where these groups are less common.

Feeding observations and gut content analyses elucidated the pathways of movement between compartments within the food web and revealed the presence of vertical stratification of foraging among major taxa, feedback loops with large invertebrates, (e.g. tailless whip scoprions, tarantulas, centipedes) eating small vertebrates, and the existence of parallel day and night food webs; the former dominated by lizards and the latter by arboreal frogs. The food web is depauperate compared to similar mainland forests and lacks the parallel host-restricted infrastructure that characterize mainland neotropical forests (Gilbert 1980).

Preliminary studies of the vertical stratification of insects showed that much of the primary consumption within the forest canopy is by planthoppers and leafhoppers, groups which feed with sunctorial mouth parts. This indicates that previous st udies of herbivory rates based on leaf area indices may substantially underestimate actual rates of herbivory in the forest. The principal invertebrate groups involved in litter decomposition were also identified (mites, millipedes, sow bugs, fly larvae), but the importance of these groups relative to other decomposition processes (e.g. microbial and fungal descomposition, abiotic processes) has yet to be determined.

Phase I studies of leaf decomposition were designed to determine differences in decomposition rates due to season, microenvironment, and species composition of the litter. Decomposition bags placed in the field at different seasons and in different plots showed no differences in rates of decomposition. The species composition of litter samples placed in the bags also had no effect on decomposition. Differences in the rates of decomposition of leaves of different species are well documented, but these differences are not apparent in heterogeneous leaf litter. The processes which control the decompositon of leaves seem to function at a uniform rate independent of local abiotic and biotic variability. The uniformity is another indication of the homogeneity of forest processes, at least at the scale of our study.

Information obtained during the first phase has provided a basis for determing the focus of Phase II research. A primary objective of Phase II studies in the El Verde study site will be to quantify the rates of movement of key nutrients and energy among major ecosystem in major food chains will be measured to determine transfer rates at higher trophic levels. All studies will consider seasonality, day and night food webs, and vertical stratification in their sampling design. Export studies are planned which examine nutrient loss due to runoff. Research within the study site will also concentrate on the soil fauna because of their probable important contribution to overall animal biomass and litter decomposition. Experimental manipulation within the El Verde study site will be limited in scope, while those conducted at nearby locations in the Luquillo Experimental Forest will either be conducted in areas with a known history of disturbance (e.g. plantations, landslide areas) or performed in conjunction with planned U.S. Forest Service manipulations.

2.0 INTRODUCTION

The accelerated development of traditional and unconventional energy resources is producing adverse effects on ecosystems throughout the world. The nature and extent of these impacts is related not only to the type of energy development (e.g. fossil fuel, nuclear, biomass, solar, etc.), but also to the prevailing environmental conditions (e.g. annual temperature fluctuations, rainfall, elevation). Therefore, information on temperate ecosystems has limited application in tropical regions. Potential impacts on temperate zone ecosystems are relatively well known but tropical ecosystems, particularly rain forests, are understood in far less detail. Their role in the world carbon cycle and their regional significance have been documented for some systems, but the structural complexity and functional interrelationship of species (e.g. food webs, biogeochemical cycles) are poorly known and are likely to differ in major aspects from their temperate counterparts.

We are therefore investigating cycling and transport processes within a relatively simple tropical rain forest. Initial studies were conducted in the rain forest near the El Verde Field Station. In-depth studies involving experimental manipulations will be undertaken as a comprehensive overview is obtained through integration of the results of Phase I field studies with published information.

The original program plan (June 1980) was formulated prior to funding changes for fiscal year 1981. Basic objectives and overall design have not been altered, but some task elements have been eliminated, and some sampling reduced to a single season where it was felt that sufficient supporting information could be obtained from existing literature. Other subtasks were added on the basis of observations and analyses of preliminary data obtained during the first seasonal sampling period.

This document presents the modified program design and results of Phase I studies from June 1980 through October 1981. Detailed methods are included so that this report can also serve as a reference guide for future studies. Substantial and in some cases unexpected results have been obtained and important aspects of ecosystem structure have been identified which have confirmed the value of this phased approach. Section 6.0 integrates material from separate tasks and summarizes important findings.

3.0 PROGRAM OVERVIEW

It is necessary to understand the major features of ecosystem structure and function and their response to exogenous environmental variables in order to predict the effects of expanding energy technology on tropical ecosystems. Current knowledge of the source-sink role of tropical rain forest biota and the factors which regulate this role is insufficient to foretell the impact of energy development on the mobilization and release of critical elements or the ecosystem's capacity to assimilate elemental inputs.

Cycling and transport processes are being investigated in the tropical (tabonuco) rain forest at El Verde by conducting a two-phased program so that a firm data base can be established before experimental manipulations are undertaken. The long history of environmental research in the Luquillo Mountains and the existence of the El Verde Field Station in this forest provide a unique opportunity for this type of research.

Phase I studies focused on obtaining additional information on the forest ecosystem and integrating these data with published material to construct a model of elemental and energy storage and movement. Faunal components are emphasized in this phase because of the lack of comprehensive food web data for tropical forests, and because of the relative wealth of vegetation data that exists for the study area. The objectives of Phase I studies are:

1. to identify the major reservoirs and pathways of elements and energy in the forest ecosystem,
2. to identify additional aspects of ecosystem organization which are relevant to the assessment of impacts, and
3. to develop hypotheses concerning the potential effects of disturbances related to energy development (e.g. inputs of sulfur, carbon, etc.; harvesting of biomass) on cycling and transport processes.

The following tasks addressed the above-stated objectives:

1. delineation of trophic structure,

2. identification of dominant species in each food web or food web segment,

3. quantification of vertical, horizontal and temporal pattern of the distribution of identifiable functional units (species trophic groups, food web segments, etc.) of the forest ecosystem,

4. quantification of the distribution of key elements among major functional units of the system taking into account spatial and temporal considerations,

5. development of a refined forest ecosystem model which will permit simulation of cycling and transport processes, and

6. generation of hypotheses concerning the potential impacts of energy development which are both relevant to tropical forest ecosystems and testable in Phase II.

The elemental and caloric inventory provide information on key nutrients and energy value of each major class of items (fruit, leaves, feces, individual species, etc.). Faunal studies identify major reservoirs and pathways and provide preliminary data on the rate of movement for selected segments of the food web. In addition to studies characterizing study plots, the vegetation work provides a basis to compare the magnitude of elemental flow through compartments with direct movement of primary production to the decomposer compartment via leaf and fruit fall and litter decomposition.

An important result of the study is a comprehensive food web in which major aspects of the distribution and transfer of energy and nutrients are known. Testing of hypotheses generated in Phase I is likely to produce useful insights on the relationship of food web complexity to species diversity, ecosystem stability, potential regulator species, and the influence of rainfall, soil type, nutrient pools, dominant consumers, and food web structure on the overall structure of ecosystems. This information will provide an important conceptual basis for inferring the key points at which perturbations due to energy development are most likely to disrupt natural systems.

Phase II will primarily involve the testing of hypotheses, although some Phase I studies (e.g. feeding and population turnover rates) will be continued. Hypothesis testing will take several forms: 1) direct manipulation of the forest (e.g. harvesting activities in conjunction with the U.S. Forest Service), 2) comparative studies of existing plantations and managed forest areas (see below), and 3) natural experiments conducted within the forest (e.g. comparison of trophic structure in areas with and without third-order carnivores).

We pose several general hypotheses which involve comparisons between native tropical hardwood (tabonuco) forest and plantations (including those which are managed for energy production). Specifically, one can hypothesize that in the native hardwood forest:

1. productivity is higher,
2. consumer biomass is greater,
3. insect pests are less abundant,
4. food web structure is more complex,
5. nutrient cycling is more rapid, and
6. the system is more resilient to exogenous disturbances

than in plantations on the same soil types and under the same rainfall regimes. The hypotheses selected for testing in Phase II will be based on information acquired in Phase I, on a realistic evaluation of potential energy related impacts, and on available funding.

4.0 PHASE I METHODS

A compartmentalized ecosystem model (Figure 1) was used as a framework for coordinating the various task studies. Work focused on those ecosystem compartments above primary producer in the food chain for the following reasons: (1) the importance of higher trophic levels in elemental transport has already been suggested for some forests (Weir 1969), but the role of fauna in moving energy and nutrients among compartments of terrestrial ecosystems has been largely neglected (Sturges et al. 1974, Burton and Likens 1975), (2) primary production and elemental cycles have already been studied in this moist tropical forest (Odum and Pigeon 1970), and (3) the role of consumers in regulating the ecosystem (Glasser 1979) is potentially significant. For these reasons only a partial measurement of elemental transport in and out of the forest ecosystems was begun in Phase I, and values needed for the current study will be taken from the literature and/or from the work of visiting and collaborating scientists.

4.1 Sampling Design

The study area (Figure 2) was selected because of its long history of continuous research, beginning with the rain forest gamma radiation studies (Odum and Pigeon 1970), and its proximity to the established facilities at the El Verde Station. Other factors which were evaluated in the study area delineation process were the relationship to U.S. Forest Service research areas and the amount of existing disturbance from previous studies.

The overall design was stratified random. Four sampling locations (points) were randomly selected within the study area so that subsequent statistically valid analyses could be performed (Green 1979). Sampling points were selected using a grid technique (Phillips 1959). The following criteria were used in the selection of random plots:

- potential confounding factors (e.g. roads, perennial streams, previous destructive sampling) were not present within 50 m of a sampling point,

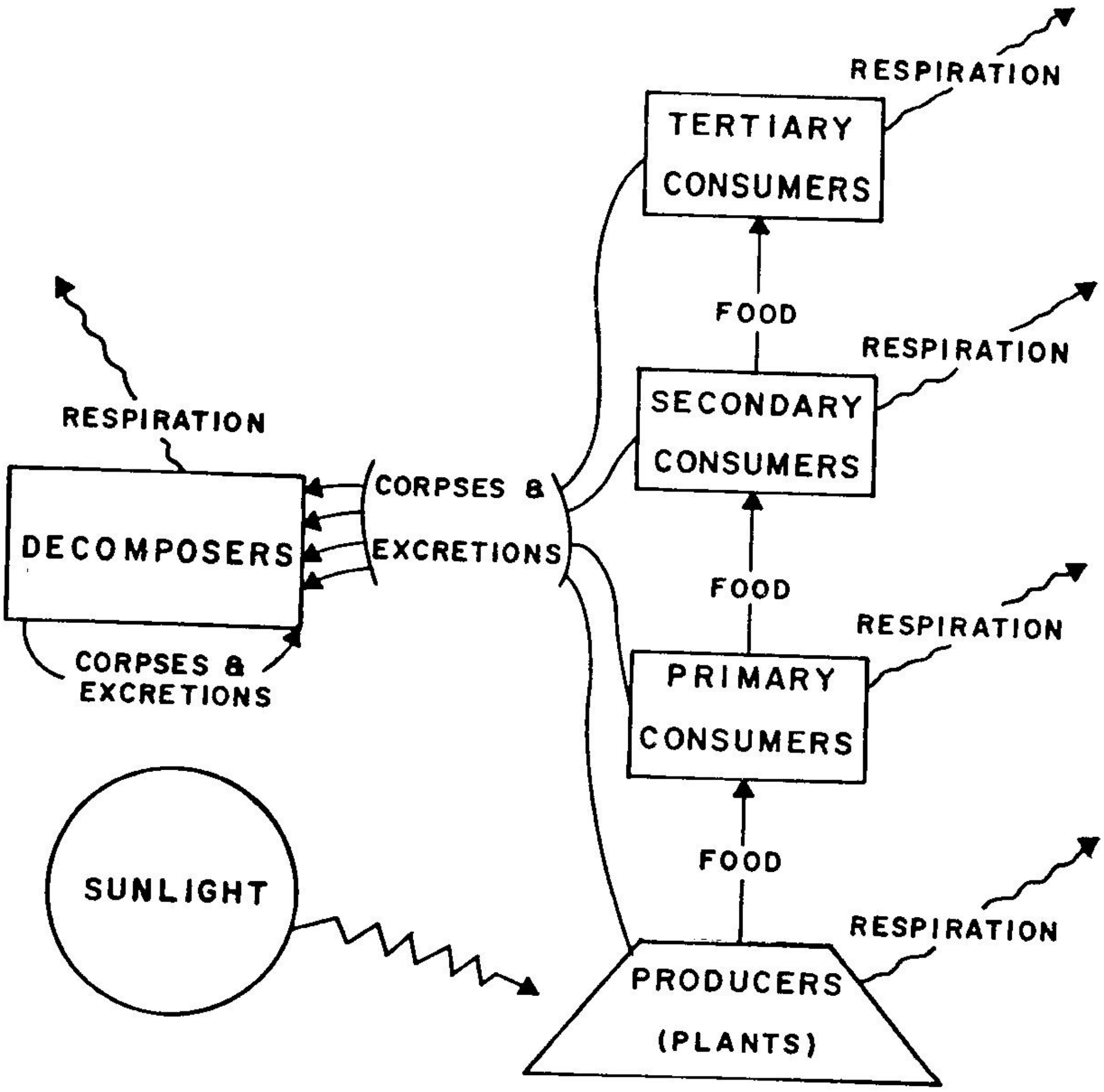


Figure 1. Generalized Ecosystem Model

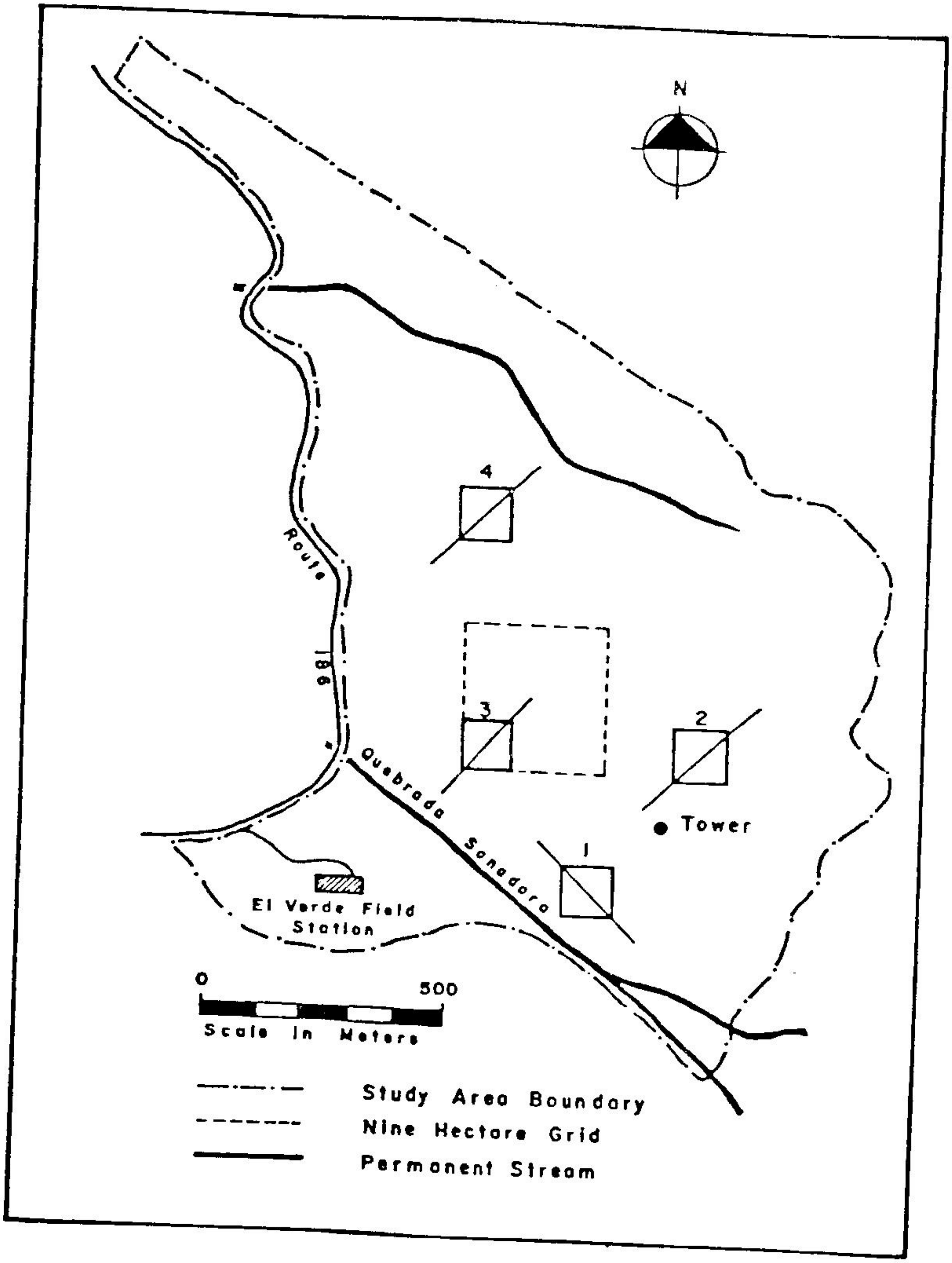


Figure 2. Cycling and Transport Program study area.

- sample points were no closer than 200 m to each other so that sampling overlap could be avoided, and
- reasonable access was possible.

The size of the area sampled at each randomly chosen point varied according to discipline (e.g. invertebrate surveys were confined to plot 3). A 1 ha plot with boundaries marked at 10 m intervals was established at each sampling point. Plot and plotless methods, transects, and detailed inventory procedures were used in Phase I investigations. Studies focused on sampling points, but included other portions of the defined study area.

Most sampling was conducted during a minimum of two seasons. Most surveys occurred during the wet and dry seasons, but additional sampling was required for some tasks (e.g. breeding bird surveys). The timing of field surveys was coordinated to avoid sampling interference yet maintain a close temporal correspondence among field studies.

4.2 Task Methods

Each task and subtask is described as a separate entity within the overall Phase I sampling design because of the variation in pertinent information already available for different disciplines. The tasks were of varying durations. Most field studies were completed by October 1981. Some studies are being continued with modifications into Phase II (e.g. growth and population turnover of key species). Although the data acquired should be of immediate value, they are intended to provide a basis for long-term in-depth studies continued under Phase II of the cycling and transport program.

4.2.1 Physical Phenomena

Basic information on physical aspects of the environment is necessary in order to interpret biological observations and to provide baseline data for Phase II studies. Specific objectives were:

- to collect pertinent weather data to be dused in evaluating information collected from other tasks
- to document seasonal and other temporal changes within the study area

Materials

- rain gages (at El Verde Station and tower)
- thermometers and hygrothermographs (at El Verde Station and four levels at the tower)

4.2.2 Elemental Inventory and Energy Studies

Objective: To construct an inventory of biologically significant elements present in tissues of the most abundant plant and animal species and to determine the energy content of these tissues

All specimens collected were chopped with scissors and dried in an oven at 70°C until constant in weight. The residue was made homogenous by grinding in a Wiley mill using a #40 mesh screen. Frogs and lizards (within species) were divided according to sex and pooled. Bats and birds were sufficiently large and were analyzed individually. All chemical analyses were run in duplicate to ensure reproducibility.

The life ions Ca^{++}, Mg^{++}, Na^{+}, and K^{+} were measured using a Model 404 Perkin Elmer atomic absorption spectrophotometer. Samples were placed in porcelain crucibles and ashed overnight in a Thermolyne muffle furnace incrementing temperature slowly up to 600°C. After cooling in a desiccator and weighing to determine the amount of nonvolatile matter, the crucibles were placed in a hot water bath and the residues allowed to dissolve in 50% HCL for one hr. Each sample was then filtered through Whatman #42 paper under suction and taken up to a known volume with double glass-distilled water.

All the water used in this study was double distilled in a Tandem 3 gal Corning water still using water pre-filtered through activated charcoal.

Phosphorus was measured with an adaptation of the method of Chapman and Pratt (1978). Orthophosphates present in the acid soluble fraction of the ash residue react to form a yellow color when exposed to the salts ammonium vanadate and ammonium molybdate under acid conditions. Color intensity becomes stable within one half hour and is measured at 470 nm. Light absorbance determinations were performed in a Zeiss PM-2 UV-VIS single beam spectrophotometer equipped with a self cleaning cell.

Nitrogen was determined by the micro-Kjeldahl procedure using a modification of the titrimetric protocol presented by the EPA Methods Handbook (1979). All biochemical forms of this element are converted to ammonium sulfate by digesting a sample suspended in conc. H_2SO_4 in the presence of a mixture of sulfates. The ammonium ion is then transformed into ammonia gas by the addition of strong alkali and distilled into boric acid. The resulting basicity is titrated with standardized H_2SO_4.

Calorimetry was performed according to Parr (1978) using a model 1341 plain oxygen calorimeter fitted with a Model 1108 oxygen bomb.

Sulfur was measured using an aliquot of the bomb washings following the turbidimetric procedure of the EPA Methods Handbook (1979). In this method sulfates produced as a result of combustion in an oxygen atmosphere are removed from solution in the form of their barium salt, the resulting turbidity being proportional to their concentration.

4.2.3 Vegetation Studies

Analysis of the vegetation was designed to determine the variability within the tabonuco forest type by measuring important storages and flows. These baseline data are to be used in the planning of Phase II experimental research.

4.2.3.1 Plot Characterization

Certain types of information were needed in order to provide a basis for interpreting floral and faunal data and for designing the future investigations. Techniques were as follows:

Subtask 1. Minimal Area

Objective: To determine the optimal plot size in which species composition of the area is adequately represented

A minimal representative area is defined as that area in which a 10 percent increase in size will yield a 10 percent or less increase in the number of new species. Two areas of the tabonuco forest in El Verde were selected at random and the nested plot technique for determining minimal area was used (Mueller-Dombois and Ellenberg 1974). The initial plot size was 5x5 m. Each additional plot was double the size of the previous plot (Figure 3).

All trees 5 cm dbh were identified and included in the study. The minimal area as defined above was determined.

Subtask 2. Structural Analysis

Objective: To determine standing crop for each species and for all species in each of the four plots

Plot 3 (Figure 2) was selected as the best representative of the four forest plots and thus the most thoroughly studied. PVC tubing was used to establish a 10x10 m grid in a 1 ha area (plot 3). All vegetation $\geq$ 10 cm dbh was identified, mapped, dbh measured, and tagged. A sub-sample of this plot was selected to be analyzed as above within a 5 m radius of each twenty randomly located litter baskets. Comparisons were then made between the total plot analysis (10,000 m^2) and the subsample (1570 m^2). Plots 1, 2, and 4 were structurally analyzed as in plot 3 using the sub-sample technique. Basal areas (m^2/ha), densities (ind/ha) and species composition were determined and compared.

4.2.3.2 Phenology

Objectives: To look for temporal differences in the flowering and fruiting patterns of species among plots

To determine importance of the contribution of each species to flower and fruit fall

Among plot comparisons of flowering and fruiting patterns were measured using materials collected in the litterfall baskets (see section 4.2.3.3 for litter sampling information).

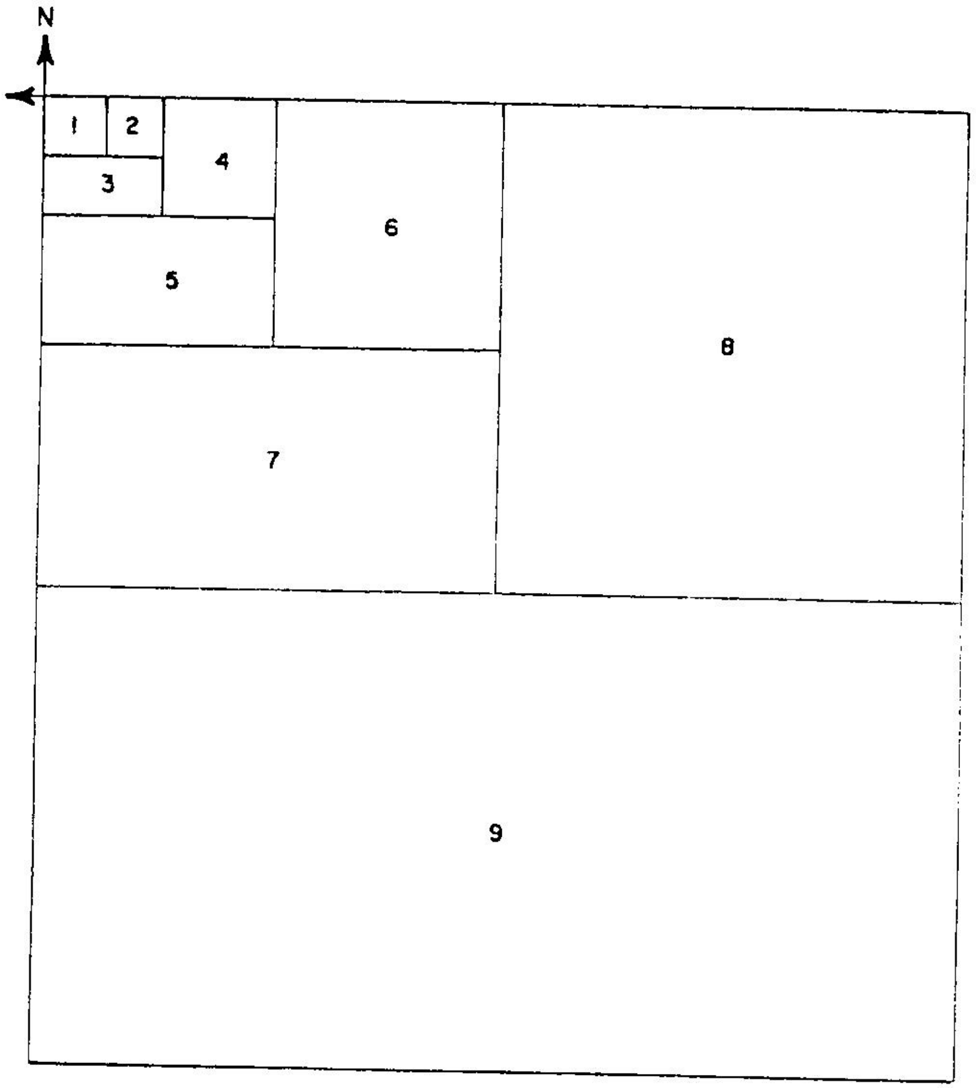


Figure 3. Sampling design for minimal area study.

Collections were made bimonthly. The mid-month collection was separated into general categories of flowers and fruits. Collections at the end of each month were separated by species into the same two categories. Each component at each collection was counted, dried at 70°C for 72 hours, and weighed. Wet season-dry season samples were stored by species and by plot for future caloric and element content.

4.2.3.3 Litter Fall

Objectives: To determine seasonal pattern of litter fall as a whole and for individual species

To detect differences between sites for total and species litter fall

To compare values of litter fall from the current study with data from other years and sampling locations at El Verde

Twenty 1 m^2 galvanized hardware cloth baskets lined with 1 mm mesh fiberglass screen were placed in each of the four plots. Locations of the four litter fall transects were randomly selected at each site with 10 m intervals between potential transect lines. Five baskets were randomly placed along each transect (Figure 4). Each basket was placed at least 10 cm from the forest floor (30 cm where possible) and leveled.

Mid-month collection of litter fall was separated by basket into leaves, flowers, fruits, wood and miscellaneous items. Each component at each collection was counted, dried at 70°C for 72 hrs and weighed. Wet season-dry season samples are awaiting analysis for caloric and mineral content.

4.2.3.4 Loose Litter (Litter Standing Crop)

Objectives: To compare seasonal differences in the ground litter storage

To determine variability among plots in the ground litter component

Loose litter samples (0.25 m^2) were collected at random in each

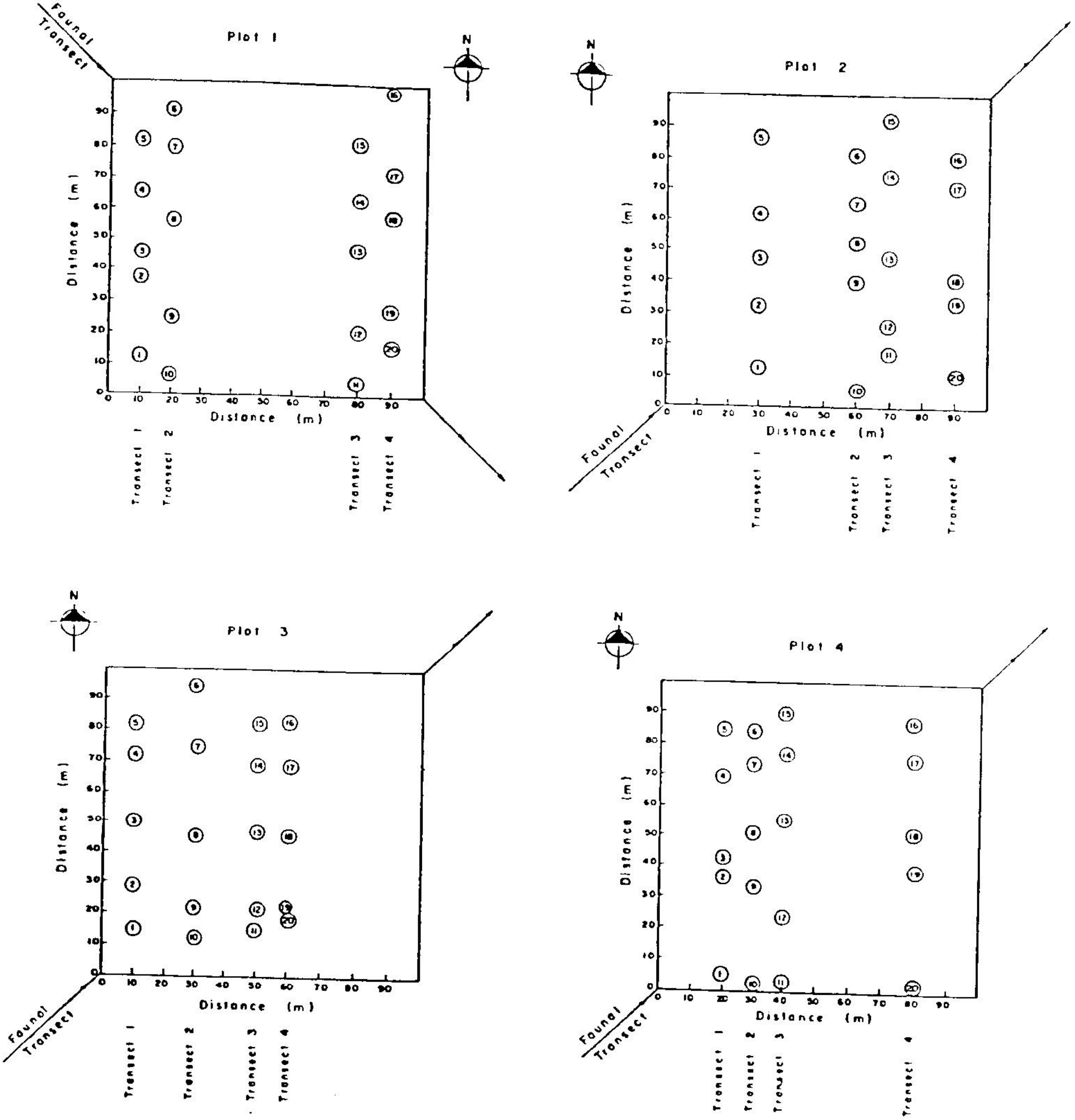


Figure 4. Vegetation sampling locations within study plots.

plot each season. Forty samples (two at each litter basket) were collected in each plot (160 total samples) during the dry season. Twenty samples (one at each litter basket) were collected in each plot (80 total samples) during the wet season. The wet season decrease in sample number was due to a smaller than expected sample variability in the dry season as well as to personnel and processing constraints.

Collected material was separated into wood and miscellaneous components, dried at 70°C for 72 hrs, and weighed. Due to the rapid decomposition of ground litter, the miscellaneous component contained all plant parts except wood and could not be successfully separated further. Wet and dry season samples from each plot were reserved for future caloric and mineral analysis.

4.2.3.5 Decomposition

Objectives:	To measure seasonal differences in decomposition rates of freshly fallen leaves
	To compare between-plot variability in leaf decomposition rates
	To determine site and species heterogeneity effects on rates of decomposition

On a single day during the dry season (25 March, 1981), all leaves that had fallen in the preceding 24 hrs (identified by the light color of the petiole abscission area; Zucca, pers. obs.) were collected from the 1 ha area in plot 3. The leaves were separated by species and allowed to air dry overnight to remove surface moisture. After drying, the freshly fallen leaves of a species were weighed and the percent of total weight of leaves collected was determined for each.

The 13 most common species were placed in decomposition bags in proportion to their occurrence in the sample. The remaining species (25) were put in a miscellaneous category and randomly selected for placing in a decomposition bag.

Bag size was 20x25 cm and bags were constructed of 1 mm mesh fiberglass screen. Sides were sewn closed with large enough gaps to allow entrance by macrodecomposers but care was taken in handling to assure no loss of leaf material.

One hundred seventy bags were filled with 10 g of representative leaf material. Five bags were placed on the ground near each of 20 randomly located litter baskets (80 bags total). In addition, 80 bags were placed in a topographically homogeneous area (plot X). Ten bags were reserved for zero time wet weight-dry weight measurements.

The species leaf composite approach to decomposition was designed to measure total plot decomposition at a specific time. Placement of bags at the litter baskets and in a homogeneous area was to establish a control for differences in topography (and presumably microenvironment).

Ten randomly selected bags were collected from both plot 3 and homogeneous plot X at intervals of 7, 14, 28, 60, 120, 240, 480 days. Bags were dried at 70°C, weighed and percent of original dry weight remaining was determined. The decomposed leaves were reserved for future caloric and mineral analysis.

The same procedure was conducted in May, 1980, with leaves from plot 3 placed as above in plots 3 and X (identified in Table 1 as 3a and 3ax). Leaves from plot 4 were placed in plots 4 and X (identified in Table 1 as 4 and 4x). The only difference from the initial procedure was a change in the number of bags. Due to the small weight variability of the initial study, 40 bags were placed in each plot and five bags collected at each interval. The May study was designed to detect variance in decomposition rates resulting from differences in species composition, season or microenvironment.

Finally, during the wet season in October, 1981, a decomposition study in plot 3 (identified in Table 1 as 3b and 3bx) was conducted as before to detect seasonal decomposition differences.

4.2.4 Faunal Studies

The roles of animals in ecosystem structure and function can be effectively evaluated by combining energy flow and nutrient cycling studies. Recent work in temperate forest ecosystems has provided

Table 1. Decomposition values (per cent original dry weight; standard error in parenthesis).

SAMPLES*

Days	3	3x	3a	3ax	3b	3bx	4	4x
7	12(2)	7(2)	10(1)	14(3)	12(2)	11(4)	14(2)	11(3)
14	22(2)	15(1)	17(2)	15(2)	19(1)	20(1)	18(4)	12(2)
28	26(1)	18(2)	18(3)	18(2)			19(3)	21(1)
60	37(1)	29(2)	32(2)	28(1)			35(5)	34(1)
90					39(3)	36(3)		
120	43(3)	42(1)	44(3)	42(2)	45(3)	46(3)	51(5)	47(3)
240			73(3)	70(3)			71(4)	77(1)
300	68(2)	66(2)	65(5)	67(4)			70(2)	72(6)

*Key to the sample designations

Leaves collected and decomposition bags placed in field

March 1981
3 = leaves from plot 3; placed randomly in plot 3
3x= leaves from plot 3; placed in topographically homogeneous plot x

May 1981
3a= leaves from plot 3; placed randomly in plot 3
3ax=leaves from plot 3; placed in plot x
4 = leaves from plot 4; placed randomly in plot 4
4x= leaves from plot 4; placed in plot x

October 1981
3b= leaves from plot 3; placed randomly in plot 3
3bx=leaves from plot 4; placed in plot x

valuable information on the roles of animal populations as nutrient "sinks" and as agents of nutrient transport (Weir 1969, Sturges *et al.* 1974, Burton and Likens 1975).

Because of their high turnover rates at relatively high ambient temperatures, underestimating the importance of organisms with short life spans and low standing crops in cycling and transport processes is even more likely in tropical systems than in temperate systems. The role of consumers as ecosystem regulators is potentially important. The Phase I faunal studies were designed to investigate these possibilities in the tropical forest ecosystem at El Verde.

The major faunal sampling effort was aimed at obtaining information on the food habits and general abundance of animals. From these data emphasizing top carnivores and herbivores a comprehensive food web has been constructed. Initial food web analyses have defined major pathways rather than focus on parallel food subwebs (Paine 1966, Gilbert 1980) which may or may not be important structural units in this insular tropical rain forest.

Studies focused on those intermediate consumers serving as principal diet items for higher order carnivores. Attempts will be made to estimate population turnover rates for key (i.e. abundant, frequently eaten or large) consumers in Phase II. Because of the large number of different intermediate consumers, their roles and rates will have to be estimated in a pooled fashion from differences between rates of primary productivity litter fall and decomposition and consumption rates of top carnivores.

The faunal studies ranged from highly diversified qualitative collection (e.g. species inventory) to more selective sampling aimed at relative abundance to highly specialized quantitative sampling aimed at key species (e.g. population estimates of birds and lizards). Relative abundance and absolute abundance data were combined to refine portions of the food web. Turnover estimates plus metabolic data, as available, will be used to quantify flows. Because of expected seasonality some types of sampling were continued throughout the entire period of study. However, with each successive sampling period, more effort was placed on relative and absolute abundance estimation for key species and species groups rather than upon the identification of new species.

4.2.4.1 Invertebrates

The invertebrates (mostly insects and mites) are an important part of the Luquillo Forest ecosystem. Chief among problems has been the proper identification of the multitudes of species inhabiting the forest. Most are small, fragile, inconspicuous forms that inhabit virtually all areas of the ecosystem. The number of identified species found in the vicinity of El Verde Field Station is at least 1200 (Drewry 1970) but the true number is probably greater than 3000. Many authors (e.g. Janzen and Schoener 1968; Allen et al. 1973; Janzen 1973a, 1973b; Janzen et al. 1976; Denlinger 1980) in reporting their ecological studies have identified forms to "morpho-species", or recognizably different kinds. Since one of the goals of this study has been to determine the important invertebrate components of the food web, we have tried to identify most taxa to the species level. Our success has been directly proportional to the amount of taxonomic literature available for Puerto Rican arthropods. Some groups, such as the Auchenorrhynchus Homoptera are fairly well known because they are common and conspicuous. Other groups, e.g. the mites and some Diptera, are poorly known and due to time (1 yr) and budget limitations, we have been forced to deal with these invertebrates at higher categorical levels such as families and orders.

A reasonably complete conspectus of the important groups of invertebrates inhabiting the Luquillo Rain Forest is currently not available and less can be said about their seasonal abundance and population turnover rates. However, ongoing studies on the vertical distribution of flying insects in the rainforest, macroinvertebrates associated with leaf litter decomposition, and gut analysis of four species of *Anolis* lizards have yielded important information on the role played by many macroarthropods in the food web. These findings also corroborate various samplings of the invertebrate fauna we have conducted at various times throughout the year.

In addition to the curated research collection at the El Verde Field Station, the following taxonomic references were helpful in identifying invertebrates: invertebrates in general - Brues _et al_. 1954, Hickman 1973; spiders - Kaston 1978, Petrunkevitch 1929, 1930a, 1930b, Velez 1971; sowbugs - Velez 1966a; millipedes-Velez 1966b, centipedes - Santiago and Velez 1974; insects in general - Borror _et al_. 1976, Borror and White 1970, Waterhouse _et al_. 1970; springtails - Mari Mutt 1976, Wray 1953; Hemiptera - Barber 1939, Capriles 1969; Homoptera - Caldwell and Martorell 1950a, 1950b, Ramos 1957; Coleoptera - Arnett 1968, Boving and Craighead 1930; ants - Lavigne 1970, Smith 1936; insect larvae - Peterson 1948, 1951. All specimens were examined under a Wild M-5 binocular stereoscopic microscope. Phase I work was divided into the following subtasks:

Subtask 1: Vertical Transect Sampling

Objectives: Determine dominant (by relative abundance) groups of flying insects during a two week sampling period in the rainy season

Determine significant differences, if any, between mean mean numbers of insects among vertical strata and between day and night

Nineteen 5 oz plastic cups, each a meter apart, were covered with "Tanglefoot" sticky trap adhesive and suspended on a string parallel to the El Verde Tower. Samples were changed at 0900 and 1800 hrs over a two week period (10 days, 8 nights) excluding weekends from 9-22 June 1981. After identification of invertebrates was completed, results were tabulated and mean numbers were compared using a one-way analysis of variance (ANOVA) and sum of squares simultaneous testing procedures (SS-STP) (Sokal and Rohlf 1970).

Subtask 2: Macroinvertebrates Associated with Leaf Litter Decomposition

Objectives: Determine suspected macrodecomposers of leaf litter for further study in Phase II

Determine possible changes in species make-up through time, i.e., if species succession occurred in leaf litter

Ninety seven 10 g fresh weight leaf litter bags were constructed and placed in plots 3 and 4 representing vegetation types typical of those areas. Bag numbers 3a and 3x contained leaf litter representative of plot 3 and 4 and 4x representative of plot 4. Bags 3a and 4 were returned to their respective plots, but bags 3ax and 4x were placed in homogeneous vegetation areas described in section 4.2.3.5. Five bags from each sample (total 20) were collected after 7, 14, 28, 60, and 120 days and the contents were placed in Berlese Funnels. All arthropods extracted were preserved in 70% ETOH and identified to lowest taxonomic category. Since leaf decomposition occurs most rapidly during the first month (section 5.2.3.5) intensive sampling was restricted to that time frame. Each sample consisted of five bags except for 60-day 4 and 4x which contained four and three bags respectively.

Subtask 3: *Anolis* Food Habits

Objectives: Determine if different species (*Anolis cuvieri*, *A. gundlachi*, *A. evermanni*, *A. stratulus*) show preferences for different invertebrate groups

Determine diet overlap, if any, among *Anolis* species

Determine if *Anolis* are obligate carnivores as has been stated in the literature

Determine if quantitative differences of prey length and volume occur between wet and dry seasons of same species of *Anolis*

A series of specimens for each species (Table 2) was collected during wet and dry seasons and stomachs were removed and preserved in 70% ETOH. Because *A. cuvieri* is a relatively rare species, their stomachs were pumped (see Sexton and Bauman 1972 for details) and the lizards were weighed, measured and released. No *A. cuvieri* were found during the dry season (Table 2). Male *A. stratulus* were difficult to obtain during the wet season and this explains their low sample size. *Anolis evermanni* also occurs along the margins of rivers, therefore 20 *A. evermanni* (10 male, 10 female) were collected from the Río Sonadora or surrounding area so that they could be compared with forest specimens. The entire contents of each stomach was examined and identified to the lowest taxonomic category (to species, if possible) and length

Table 2. Sample sizes of _Anolis_ lizards used in evaluating food data.

		dry season	wet season
A. cuvieri	♂	-	1+
	♀	-	9+
A. gundlachi	♂	10	10
	♀	10	10
A. evermanni	♂	10	19*
	♀	8	20*
A. stratulus	♂	8	4
	♀	10	9

+data combined

*includes 10 specimens from edge of Río Sonadora, a non-forest habitat.

(mm) and volume (length times width times height; mm^3) for each specimen was calculated or estimated. Data for A. cuvieri were probably underestimates because all of the stomach contents may not have been removed by pumping.

4.2.4.2 Amphibians and Reptiles

These poikilothermic vertebrates are conspicuous components of the animal community in Puerto Rican rain forests. Considerable data are available for some groups, but additional information is needed in order to evaluate their role in cycling and transport processes. The basic data required are: 1) elemental and energy content, 2) status in food web (food habits and predators), 3) biomass, and 4) population and feeding turnover rates. Phase I studies focused on acquiring information for the first three areas and identifying species and groups for continued investigation in Phase II. Phase I work was divided into the following subtasks:

Subtask 1: Species Inventory

Objective: To determine the presence and general abundance of all amphibian and reptile species inhabiting the study area

Intensive searches were conducted at randomly selected locations and in particular microhabitats (e.g. boulder areas) periodically throughout Phase I field studies. Random observations were also noted. Surface debris and litter were overturned in order to locate secretive and fossorial species. The species, location, date, and activity was recorded for each individual observed.

Subtask 2: Presence and Relative Abundance of Amphibians

Objective: To determine the species composition and frelative abundance of amphibian (anuran) species within the study area in order to identify important species and to in correlate information collected at study plots with the more detailed information being collected by Dr. M. Stewart and her colleagues in adjacent areas of the forest

Surveys were conducted along transects (50x2 m) through the four randomly selected plots within the study area (Figure 2). Each transect was surveyed on three separate evenings during the wet season.

The sex (where possible) and size class was recorded for each species. Species heard calling outside the transects but within plots were also noted. Relative abundances were then calculated.

Subtask 3: *Anolis* Food Habits

Objective: To determine the types of food taken, frequency of occurrence, and percentages of food for each species

Detailed methods for food habit analyses are provided in section 4.2.4.1, Subtask 3.

Subtask 4: *Anolis* Population Densities

Objectives: To obtain minimum and relative population density estimates dfor common species of *Anolis* at four randomly selected locations within the study area

To estimate the absolute density of the canopy species, *Anolis stratulus* at the tower within the study area

Minimum and relative population densities - A permanent transect 150 m long was estabished in each plot, extending from the center diagonally through the plot along existing bird transects (Figure 2). Each transect was surveyed by slowly walking the marked line on three occasions: morning (0700-1000), midday (1000-1430), and afternoon (1430-1800) during wet and dry seasons. The species, sex (or size class), and distance to the centerline were recorded for each lizard observed. Relative abundances were computed and minimum population densities were calculated according to Frye's strip census technique (Overton 1971):

$$T = \frac{CA}{2Lh}$$

$\bar{h}$: average perpendicular distance between observed animal and transect centerline

C: correction factor for units of measurement

L: transect length

A: area of study site

T: estimated population density

t: number of animals observed on transect

Population density estimates for *Anolis stratulus* - Data were obtained from multiple mark and resight data collected during the dry season (February - March) of 1981. Vertical transect surveys were conducted from the tower during midday (1000 - 1430) for four days within a two week period. Transects were not conducted during periods of rain. Each individual was marked with paint (a different color for each day) and hot branded with an individual mark. Lizards were captured and marked on each of the first three days, but only observed on day four.

Mark and resight data were analyzed using the Jolly-Seber, Manly-Parr, and Lincoln-Peterson techniques (Manly and Parr 1968, Jolly 1965, Overton 1971). Because transects were conducted vertically, results are expressed as a point sample with the area surveyed calculated from the maximum observation radius from the tower, and population estimates projected to ground level.

Subtask 5: Vertical Distribution of Anoline Lizards

Objective: To determine the vertical distribution of common lizard species in the rain forest

Casual observations from the 22 m tower in the study area (Figure 2) suggested that the three common *Anolis* lizards differ in their vertical distributions. To test this hypothesis, vertical transect surveys were conducted at the tower during Phase I studies. The following procedures were used.

Fifteen transects were conducted at each of three times of day: morning (0700-1000), midday (1000-1430), and afternoon (1430-1800) for a total of 45 transects during wet season 1980 (September - November) and again during dry season 1981 (January - March). Each transect was surveyed by slowly walking up the tower and recording the species, sex (where possible), height above ground level (marked on the tower), distance from transect centerline and date/time of day for each lizard observed. Mean sighting distances were calculated for each species and used to compute the relative number of lizards at each meter interval for the 22 m transect for each species. Data were analyzed by species, season, and time of day in order to determine what, if any, differences existed which might be relevant to the trophic structure and organization within the forest.

Subtask 6. Anolis Population Growth and Turnover Rates

Objective: To obtain reliable estimates of population turnover and growth rates for Anolis stratulus

Pertinent data for this important species are presently unavailable. Individual lizards captured during the mark and resight studies were weighed and measured at time of capture. Periodic visits are being conducted at the tower to record the proportion of marked to unmarked lizards present. Individual marked lizards are periodically recaptured and are reweighed and remeasured. These surveys will continue into Phase II. Information on population turnover rates, longevity, and growth rate will be calculated from these data.

4.2.4.3 Birds

Five subtasks were carried out in the avifaunal studies by methods described in the original work plan and modified in the Phase I Progress Report (January 1981). A complete description of the methods for each subtask is given below.

Subtask 1: Population Density

Objective: To obtain reliable population estimates for each species in all sites studied and to detect changes in population density throughout the year

Single avian census techniques are often insufficient to estimate population densities of the wide variety of species found in tropical habitats (Waide *et al.* 1980, Waide and Hernández 1982). To accommodate the diversity of behavioral types and vertical partitioning found in tropical birds, multiple census techniques are often needed (Terborgh and Weske 1969). In the mineral cycling and transport study, three different census techniques were used to obtain absolute and seasonal estimates of population density.

Transect counts - A diagonal 300 m transect line was established in each of the 1 ha study plots and marked at 10 m intervals with stakes and plastic flagging (Figure 2). Each month, transect counts were conducted for two days in each site. Counts began at 0730 and consisted of an outgoing traverse of the transect line, a five-minute wait, and a returning traverse. A single observer conducted the July-September counts in 1981 and two observers divided the rest of counts. After the termination of one year of monthly counts, subsequent sampling was conducted at two month intervals (August and October 1981). Afternoon counts beginning at 1500 were run in July, October and January.

Data recorded during each count included date, location, time, observer, and weather conditions. Each bird detected was identified to species and the perpendicular distance to the transect line was estimated within the following distance classes: 3, 6, 9, 12, 15, 30, 60, 120 m. Detections were not recorded if they were more than 120 m from the transect line or more than 30 m ahead or behind the observer. Further data included position along the transect line, side of the transect line, and height of the bird if it was seen. Detections by sight, song and call were recorded separately. A sample data sheet is shown in Appendix I.

Population densities were calculated separately for each detection class following Emlen (1971). Results are reported separately and as the sum of detections by sight, song and call. Observations were summed over the entire sampling period to determine effective detection distance which was then used to calculate densities in each month for each plot. Currently, further analysis is underway using a computer program (TRANSECT) developed by Burnham _et al_. (1980).

Mist nets - Sampling with nylon mist nets is often effective in determining abundance for shy or unobtrusive species that are underestimated by observational techniques. A net line was established in each plot bisecting the transect line. Mixtures of 30 and 36 mm standard 12 m black mist nets were strung end-to-end on poles made of conduit tubing. Nets sampled the space from 15 cm to 2 m above the ground. During September-October 1980, nets were opened from dawn to dusk on consecutive days, weather permitting. All birds captured were marked with colored plastic leg bands or by clipping a combination of tail feathers. Data collected are shown in the sample data sheet in Appendix I.

Sampling continued until the day's catch of new birds was less than half the mean catch of previous days. Relative population estimates for commonly caught species were calculated by regressing capture rate on cumulative number of birds caught (Terborgh and Faaborg 1973, MacArthur and MacArthur 1974).

Spot maps - A grid with lines at 30 m intervals was established in a 9 ha area which included plot 3 (Figure 2). Beginning in February, 1981, sampling with mist nets was conducted along alternate grid lines. All birds captured were marked as indicated above. Two productive nets near a bathing area were used more intensively. Sampling concluded in April.

In June and July, the entire grid was traversed by a single observer on 10 different days. The location of each singing bird was recorded on maps of the gridded area. At the end of the sampling period, data for each species were transferred to master maps of the study area. Territories were delineated on the maps around clusters of observations with special weight given to territorial disputes and marked birds. The minimum requirement for the definition of a territory was three observations of a singing bird on different days (Int. Bird Census Comm. 1970). Number of whole and fractional territories were totaled for each species and doubled to account for females. Absolute density in individuals/ha was calculated by dividing by the area in ha of the study site.

Subtask 2: Feeding Behavior

Objective: To accumulate sufficient observations of feeding to test for differences between species, sites, seasons and individuals

Approximately equivalent amounts of time were spent collecting foraging data in each study plot. In addition, incidental observations were made during transect censuses and between study plots. A timed observation was made of each bird found foraging. Location, date, time, weather and observer were routinely recorded for each individual. Time of observation, tree species, habitat compartment, activity, canopy, tree, and bird height, type of movement, direction and distance of movement, substrate attacked, prey taken and perch diameter were the foraging parameters. Each individual was followed through at least one feeding attempt or until lost from sight. A sample data sheet is shown in Appendix I.

Foraging data collected in the Luquillo National Forest by Cameron and Angela Kepler is available for comparison with the current study. Data will be compiled and analyzed on an Apple II computer using techniques described by Waide (1981). Statistical treatment will be designed to test for 1) seasonal differences within species, 2) differences between sites for each species, 3) differences between species, and 4) differences between individuals of the same species.

Subtask 3: Diet and Weight

Objective: To determine differences in diet and weight between species, sites, seasons and individuals; to describe the avian section of the food web

All birds captured in connection with Subtask 1 were weighed and 30 stomachs were sampled with antimony potassium tartarate emetic (Prys-Jones et al. 1974, Tomback 1975). In addition stomachs of 45 individuals of nine species collected for elemental analysis were examined for their contents. All birds were weighed on an Ohaus Triple-beam balance to the nearest 0.1 g.

Birds collected for elemental analysis were frozen within two hours of death. During processing for chemical analysis, entire stomachs were removed and opened and their contents were placed in 70% ETOH. Birds captured during marking studies had 0.1-0.5 ml of 1% antimony potassium tartarate solution introduced into their stomachs via a syringe and tygon tubing. Each bird was placed in a closed container for 15 min and the regurgitated stomach contents were collected with forceps and placed in 70% ETOH. The contents of stomachs were separated into animal and vegetable remains and proportions of each were estimated on a relative volume and per item basis. Animal remains are being identified to the lowest taxonomic level possible by

R. Garrison. Seeds were identified using a reference collection established for that purpose by A. Estrada.

Construction of the avian section of the food web will use data from foraging observations, stomach analyses, published literature and unpublished field observations of other workers. A compartmentalized model will be developed into which individual species will be placed according to the proportion of their diet derived from each compartment. In addition, a trophic diagram will be developed showing the amount of biomass assignable to different trophic levels.

Subtask 4: Materials Discharge

Objective: To obtain reliable estimates of the amount of fecal and regurgitated material produced/individual of each species per unit time

Although completion of this subtask has been postponed until Phase II, the methods to be used are presented here. Mist-netted birds will be placed in holding cages for 1) 1 hr during the day and 2) overnight. Fecal and regurgitated material will collected, dried and weighed. Samples of fecal material will be combined and analyzed to determine mineral content. Using observed rates of defecation in the wild and in birds caged overnight, the amount of material returned to the environment/individual/unit time will be calculated.

Subtask 5: Elemental Content

Objective: To obtain reliable estimates of the elemental content per unit weight of 1) whole stomach contents and individual food items, 2) body tissue, 3) feathers and 4) feces and regurgitated material

Key food items will be identified in Subtask 3 for important species in the food web. Chemical analysis of specific fruits and seeds and general analyses of invertebrates are under way and results are reported in Section 5.2.

Forty-five individuals of nine species have been analyzed for energy and mineral content of feathers and body tissue. Specific methods are given in Section 5.2. Results of these analyses used in conjunction with data on molt and population turnover will allow the development of models of mineral and energy flow at individual, population and community levels.

4.2.4.4 Mammals

Objective: To determine the presence and general abundance of mammal species within the rain forest study area

The role of mammals in the rain forest ecosystem is of interest primarily because the larger species (e.g. Indian mongoose and roof rat) have been introduced by man and all native inhabitants are bats. Field studies focused on determining the species present, their general abundance, and identifying their place in the overall trophic structure.

Bats - Night surveys were conducted using mist nets (30 mm and 36 mm mesh). Vertical nets were erected in the opening at the station during November and December, 1980, and July, 1981. Horizontal nets were rigged in plots 1 and 2, at two forest locations near the field station facilities, and on the Rio Sonadora foot bridge east of the field station. Nets were opened at sunset and closed at dawn to avoid capturing birds. Nets placed in remote locations (plots 1 and 2) were closed at 2300. For each bat captured, the species, sex, weight, tarsus and forearm measurement were recorded. Some specimens were retained for calorimetry and nutrient analyses and the remaining individuals were released. Food habit information was taken from the literature, although some data was obtained from gut analysis of a single Stenoderma rufum captured at a low net in July 1981.

Small mammals - Two traplines of 10 Sherman live traps (3X3X9 in) each were placed parallel to each other between plots 3 and 4. All traps and traplines were spaced at 15 m intervals. Lines were surveyed for three consecutive days and nights from 18 to 21 November 1980. Traps were checked daily and rebaited as necessary.

Large terrestrial mammals - Twenty-five Tomahawk double-ended live traps (6X6X24 in) were deployed at 30 m intervals in a 5X5 grid at plot 3. Traps were baited, opened, and checked daily for three consecutive days and nights from 22 to 24 November 1980 and again from

6 to 9 January 1981. The species and sex of each trapped individual was recorded, and each was marked with a different paint marking so that recaptures and individual movements could be detected.

5.0 RESULTS AND DISCUSSION

Initial surveys have produced substantial and in some cases unexpected results. Because these data are preliminary, integrative analyses are not possible at this time for all tasks. Results are herein reported and discussed by task.

5.1 Physical Phenomena

Daily rainfall and continuous records of relative humidity and temperature fluctuations have been collected at the El Verde Field Station since the radiation studies in the rain forest during the mid-1960's. The tower station was established in July, 1980 and will be maintained throughout the program field studies. Prior to the implementation of Phase II studies a rain fall event recorder will be installed at the tower and a wind (velocity and direction) gage and a stream flow gage may be added to the program.

5.2 Elemental Inventory and Energy

We wanted to establish normal steady-state values for chemical parameters of ecological importance to be used as "control" guidelines for studying mineral cycling dynamics and the environmental impacts of new forms of energy. The group of elements selected had to be of biological as well as geological significance and present in sufficiently large amounts to be measured with ordinary laboratory equipment. The following elements were chosen: nitrogen, phosphorus, calcium, sodium, potassium, magnesium and sulphur. Gross heat of combustion and percent ash were also measured.

5.2.1 Elemental Inventory

Tables 3-6 show elemental and caloric data for all groups analyzed. The ash content for the various species varied between 13 and 19%, except feathers, whose values were considerably lower, at approximately 2% of their dry weight.

Table 3. Elemental composition and caloric value of amphibians, reptiles and bats.

	Sex	N	P	S	Hg*
Eleutherodactylus coqui	M	23.41 ± .37	3.86 ± .55	.39 ± .01	4,286 ± 721
	F	23.21 ± .45	3.98 ± .15	.13 ± .01	4,399 ± 339
Anolis evermanni	M	22.48 ± .02	5.10 ± .27	.81 ± .06	4,563 ± 232
	F	19.61 ± .32	3.65 ± .03	.72 ± .24	4,269 ± 669
A. gundlachi	M	22.32 ± .22	4.99 ± .95	.85 ± .04	4,029 ± 125
	F	33.13 ± .06	4.25 ± .67	1.01 ± .02	4,652 ± 82
A. stratulus	M	20.03 ± .11	4.88 ± .02	.80 ± .08	5,779 ± 470
	F	16.36 ± .80	3.55 ± .03	.94 ± .39	5,144 ± 316
Artibeus jamaicensis	M	20.33 ± .17	4.73 ± .33	.39 ± .03	5,432 ± 373
	M	19.90 ± .75	4.28 ± .07	.88 ± .11	5,018 ± 245
	M		4.35 ± .53	.34 ± .03	5,183 ± 31
	F	15.65 ± .11	4.67 ± .03	.64 ± .19	4,768 ± 36
	F	22.35 ± .17	4.98 ± .22	.78 ± .05	4,893 ± 14
	F	16.43 ± 1.68	3.85 ± .13	1.78 ± .02	5,285 ± 395
	F	21.02 ± .39	4.41 ± .07		5,224 ± 21
	F	19.88 ± .30	4.29 ± .01	.75 ± .03	5,072 ± 68
	F	21.00 ± .19	4.83 ± .19	.53 ± .02	4,875 ± 68
	$\overline{M}$	20.12 ± .30	4.45 ± .24	.54 ± .29	5,211 ± 208
	$\overline{F}$	19.39 ± 2.72	4.51 ± .41	.70 ± .11	5,020 ± 207

Element values expressed in % of dry weight.
*Gross heat of combustion in cal/g.
± in the case of bat averages, M & F, indicate the S.D.

Table 4. Inorganic on composition of amphibians, reptiles, and bats.

	Sex	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
Eleutherodactylus coqui	M	40.56 ± .09	2.15 ± .05	6.39 ± .02	7.81 ± .07	14.51 ± 2.09
	F	38.57 ± .65	1.87 ± .05	6.35 ± .29	7.00 ± 1.09	15.15 ± .10
Anolis evermanni	M	44.07 ± .87	2.07 ± .07	6.05 ± .33	8.68 ± 1.17	18.66 ± 1.11
	F	33.55 ± .48	1.88 ± .02	5.55 ± .11	9.57 ± .41	14.53 ± .30
A. gundlachi	M	48.68 ± 1.67	2.12 ± .03	7.13 ± .48	7.68 ± 1.14	19.86 ± .04
	F	51.16 ± .16	2.03 ± .02	6.57 ± .01	5.51 ± 1.23	19.22 ± .23
A. stratulus	M	32.07 ± 4.10	1.99 ± .10	6.35 ± 1.16	7.56 ± 1.00	15.63 ± .75
	F	28.09 ± 1.83	1.71 ± .01	5.39 ± .06	7.89 ± .51	13.27 ± .11
Artibeus jamaicensis	M	47.05 ± .67	1.81 ± .04	4.21 ± .02	7.73 ± .28	19.13 ± .34
	M	43.73 ± .06	1.84 ± .11	4.55 ± .56	5.92 ± 1.26	18.34 ± .05
	M	42.30 ± 1.44	1.88 ± .07	7.88 ± .18	1.82 ± .07	17.54 ± .34
	F	46.02 ± 3.96	1.76 ± .01	4.00 ± .01	6.85 ± .92	21.09 ± 1.95
	F	43.14 ± 1.62	1.84 ± .01	4.95 ± .86	6.62 ± .20	19.80 ± 1.67
	F	38.03 ± .01	1.62 ± .01	3.72 ± .16	1.63 ± .01	15.41 ± .81
	F	40.45 ± 2.25	1.87 ± .05	6.29 ± 1.78	6.91 ± 1.18	16.21 ± .42
	F	41.95 ± .22	1.99 ± .03	4.85 ± .07	5.04 ± .02	16.03 ± .24
	F	45.69 ± 1.10	2.01 ± .02	5.02 ± .22	4.01 ± .50	17.20 ± .61
	$\overline{M}$	44.36 ± 2.44	1.86 ± .04	5.55 ± 2.03	5.15 ± 3.03	18.34 ± .56
	$\overline{F}$	42.55 ± 3.08	1.85 ± .15	4.80 ± .72	5.17 ± 2.09	17.62 ± 2.30

Inorganic ions are expressed in mg/g dry weight.
Ash content is expressed in % of dry weight.
± indicate difference between duplicate samples
from their average.

Table 5. Elemental composition and caloric value of bird tissues.

Individual	Sex	Type	N	P	S	Hg*
Ruddy Quail Dove						
800723-02	F	B	21.66 ± .21	3.58 ± .52	.70 ± .10	4,772 ± 15
		F+P	29.18 ± .30	.27 ± .01		
800723-03	F	B	22.63 ± .43	3.31 ± .12	.51 ± .05	4,635 ± 268
		F+P	28.79 ± .30	.09 ± .02	2.07 ± .09	5,432 ± 80
800723-04	M	B	23.92 ± .22	3.54 ± .10	.96 ± .19	4,933 ± 23
		F+P	28.34 ± .30	.20 ± .02	1.65 ± .49	2,413 ± 4
810310-02	F	B	21.41 ± .11			
		F+P	28.05 ± .51			
		$\overline{\text{B}}$	22.41 ± 1.14	3.48 ± .15	.72 ± .23	4,704 ± 97
		$\overline{\text{F+P}}$	28.59 ± .50	.19 ± .07	1.86 ± .30	3,923 ±2,134
Puerto Rican Tody						
801021-02	M	B	35.11 ± 2.94	4.61 ± .31		
		F+P				
801106-02	F	B	22.57 ± 1.46	5.04 ± .18	.75 ± .03	5,080 ± 18
		F+P	29.20 ± .19			
810318-51	F	B	20.82 ± .51			
		F+P	23.76 ± .66			
810318-52	M	B	24.48 ± .36	4.63 ± .04	.77 ± .10	4,507 ± 138
		F+P		.58 ± .05		
810318-57	F	B	19.74 ± .13			
		F+P	22.90 ± .62			
810318-58	M	B	20.18 ± .04			
		F+P	28.77 ± .75	.11 ± .01		
810318-60	M	B	21.95 ± 1.87			
		F+P	21.94 ± 2.04			
		$\overline{\text{B}}$	23.55 ± 5.34	4.83 ± .30	.76 ± .01	4,794 ± 405
		$\overline{\text{F+P}}$	25.31 ± 3.42	.35 ± .33		

*Gross heat of combustion cal/g.

±Indicate difference between duplicate samples except in the case of averages where it indicates the S.D.

Element and the values are expressed as % of dry weight inorganic ions are expressed as mg/g dry weight.

Pearly eyed Thrasher

Individual	Sex	Tissue Type	N	P	S	Hg*
800729-01	-	B F+P	21.67 ± .09 30.77 ± .13	4.76 ± .30 .12 ± .05	.98 ± .05 1.66 ± .34	5,139 ± 26 5,099 ± 84
800630-01	F	B F+P	20.73 ± .11 25.77 ± 1.49			
801211-02	M	B F+P	19.12 ± .19 24.48 ± .37			
801216-02	M	B F+P	21.77 ± .26 30.86 ± .69	4.80 ± .35 .15 ± .10		
810911-01	M	B F+P	18.77 ± .10 26.89 ± .41			
		B̄ F+P	20.41 ± 1.40 27.75 ± 2.92	4.78 ± .02 .14 ± .01	.98 ± .05 1.66 ± .05	5,139 ± 26 5,099 ± 84
			Red Legged Thrush			
800723-01	F	B F+P	19.41 ± .17 24.95 ± .27			
800724-01	M	B F+P	20.71 ± .16 33.43 ± .94	5.04 ± .80 .21 ± .03	.63 ± .05	4,651 ± 5
800903-01	M	B F+P	21.75 ± .86	5.34 ± .12	.75 ± .25	4,690 ± 6
801204-01	M	B F+P	17.99 ± .06 24.89 ± .22			
810910-04	M	B F+P	21.01 ± .17 27.93 ± .31			
810911-02	M	B F+P	20.90 ± .25 27.60 ± .03			
		B̄ F+P	20.32 ± 1.36 27.76 ± 3.47	5.19 ± .15 .21 ± .05	.69 ± .08	4,672 ± 19

Bananaquit

Individual	Sex	Tissue Type	N	P	S	Hg*
801110-01	M	B	17.83 ± .06	3.84 ± .79		
		F+P				
801216-01	M	B	22.03 ± .34	4.06 ± .10	.83 ± .09	5,247 ± 18
		F+P	29.60 ± .09			
810430-04	M	B	18.57 ± .41			
		F+P	23.56 ± .30			
810806-01	M	B	17.39 ± .14			
		F+P	22.48 ± .70			
810910-10	M	B	17.56 ± .70			
		F+P				
810911-05	M	B	17.00 ± .09			
		F+P	24.79 ± .18			
		B̄	18.40 ± 1.86	3.95 ± .15	.83 ± .09	5,247 ± 18
		F+P	25.11 ± 2.72			

Puerto Rican Tanager

Individual	Sex	Tissue Type	N	P	S	Hg*
801215-01	M	B	17.65 ± .15	4.36 + .07	.92 ± .05	5,006 ± 113
		F+P	25.85 ± .02			
801215-02	-	B	20.64 ± .30	4.36 ± .07	.84 ± .09	4,918 ± 95
		F+P	29.70 ± 1.09	.07 ± .02	2.75 ± .48	4,924 ± 91
801215-03	M	B	20.64 ± .13	4.49 ± .08	1.00 ± .07	5,515 ± 517
		F+P	28.28 ± .47	.04 ± .02		
810317-01	F	B			.82 ± .14	4,831 ± 47
		F+P			2.92 ± .20	5,045 ± 50
810317-02	F	B	16.87 ± .39		.83 ± .05	5,077 ± 72
		F+P				
810317-03	F	B	17.97 ± .11	5.05 ± .19		
		F+P	21.39 ± .20	.02 ± .01	1.83 ± .14	4,473 ± 67
810413-04	F	B	17.06 ± .27		.78 ± .12	5,396 ± 24
		F+P	25.50 ± .27			
		B̄	18.46 ± 1.74	4.62 ± .37	.85 ± .08	5,124 ± 273
		F+P	26.14 ± 3.17	.043 ± .03	2.11 ± .80	4,814 ± 301

Individual	Sex	Tissue Type	N	P	S	Hg*
			Puerto Rican Emerald			
801027-01	M	B				
		F+P				
801029-01	F	B		4.24 ± .05		
		F+P		.05 ± .01		
801112-01	F	B		3.95 ± .23	.52 ± .05	6,115 ± 67
		F+P				
801118-01	F	B		5.00 ± .18		
		F+P				
810318-53	M	B	20.40 ± .20			
		F+P	19.07 ± .22			
810318-54	M	B	21.55 ± .10			
		F+P	22.32 ± .22			
810318-61	M	B	20.55 ± .20			
		F+P				
		$\overline{B}$	20.83 ± .63	4.40 ± .54	.52 ± .05	6,115 ± 67
		$\overline{F+P}$	20.70 ± .15	.05 ± .01		
			B.W. Vireo			
810413-05	M	B	19.04 ± .14			
		F+P	24.57 ± .20			
810426-01	F	B	18.25 ± .92			
		F+P	27.51 ± .40			
		$\overline{B}$	18.65 ± .40			
		$\overline{F+P}$	26.04 ± 1.47			
			Puerto Rican Bullfinch			
810310-01	-	B	19.99 ± .25		.73 ± .06	4,965 ± 34
		F+P	25.04 ± .04			
Combined bird average		$\overline{B}$	20.29 ± 1.78	4.46 ± .58	.76 ± .13	5,095 ± 464
		$\overline{F+P}$	25.82 ± 2.31	.16 ± .11	1.88 ± .23	4,612 ± 614

Table 6. Inorganic ion composition of birds and their feathers.

Individual	Sex	Tissue Type	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
Ruddy Quail Dove							
800723-02	F	B	25.80 ± 1.57	1.53 ± .13	4.57 ± .11	8.67 ± .20	13.59 ± .09
		F+P		.628 ± .04	1.37 ± .01	1.82 ± .09	3.03 ± .97
800723-03	F	B	26.34 ± .96	1.53 ± .01	4.95 ± .24	7.82 ± .94	12.32 ± .05
		F+P	.357 ± .01	.349 ± .01	.931 ± .05	1.18 ± .08	3.97 ± .12
800723-04	M	B	28.71 ± 1.00	1.48 ± .10	4.77 ± .10	8.83 ± .20	13.26 ± .40
		F+P		.515 ± .06	1.34 ± .42	.966 ± .05	3.04 ± .85
810310-02	F	B		1.64 ± .19		6.39 ± .16	11.23 ± .49
		F+P		.514 ± .07	1.38 ± .50	.890 ± .03	<1
		$\overline{B}$	26.95 + 1.55	1.55 ± .07	4.76 ± .19	7.93 ± 1.12	12.60 ± 1.06
		$\overline{F+P}$		.502 ± .115	1.25 ± .22	1.21 ± .42	3.35 ± .54
Puerto Rican Tody							
801021-01	M	B		1.61 ± .10			15.40 ± .50
		F+P					
801106-02	F	B	31.36 ± 1.36	1.49 ± .02	4.95 ± .01	6.61 ± .12	15.60 ± .01
		F+P	1.37 ± .67	.110 ± .01	.286 ± .04	.352 ± .06	2.06 ± 1.46
810318-51	F	B	11.31 ± .01	1.88 ± .06		5.38 ± .24	12.55 ± .55
		F+P		.905 ± .05			1.45 ± .05
810318-52	M	B	19.96 ± 1.70	1.66 ± .01	5.17 ± .08	7.44 ±1.71	12.01 ± .19
		F+P					
810318-57	F	B	23.78 ± 1.00	1.71 ± .15		6.07 ± .63	12.90 ± .50
		F+P		.735 ± .05		1.18 ± .25	1.36 ± .05
810318-58	M	B		2.18 ± .50		9.17 ± .50	13.11 ± .50
		F+P		1.02 ± .05	2.01 ± .11	1.37 ± .24	1.56 ± .05
810318-60	M	B	20.43 ± 1.00	1.76 ± .16		8.00 ± .50	13.59 ± .83
		F+P					1.89 ± .05
		$\overline{B}$	21.39 ± 7.24	1.76 ± .22	4.04 ± 1.76	7.11 ±1.38	13.59 ± 1.39
		$\overline{F+P}$		.693 ± .41		.967 ± .54	1.67 ± .30

Pearly-eyed Thrasher

Individual	Sex	Tissue Type	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
800729-01	-	B	30.53 ± 2.00	1.47 ± .05	4.78 ± .10	9.56 ± .50	13.74 ± .72
		F+P	.715 ± .10	.451 ± .05	1.74 ± .07	1.27 ± .12	1.63 ± .18
800630-01	F	B					
		F+P					
801211-02	M	B					
		F+P					
801216-02	M	B	28.24 ± 2.00	1.77 ± .05	5.75 ± .10	7.12 ± .20	14.15 ± .95
		F+P		.610 ± .05	1.17 ± .01	.217 ± .01	3.16 ± .79
810911-01	M	B					
		F+P					
		$\overline{B}$	29.39 ± 1.0	1.62 ± .21	5.27 ± .69	8.34 ± 1.73	13.95 ± .29
		$\overline{F+P}$		.531 ± .11	1.46 ± .40	.744 ± .745	2.40 ± .77

Red-Legged Thrush

Individual	Sex	Tissue Type	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
800723-01	F	B					
		F+P					
800724-01	M	B	36.40 ± 3.00	1.59 ± .05	4.75 ± .10	9.17 ± .20	15.60 ± .13
		F+P	1.18 ± .32	.547 ± .01	1.21 ± .03	1.57 ± .12	1.65 ± .38
800903-01	M	B					
		F+P					
801204-01	M	B					
		F+P					
810910-04	M	B	21.72 ± .30	1.64 ± .07	4.32 ± .02	10.73 ± .13	15.59 ± .93
		F+P		.89 ± .03	1.18 ± .16	.770 ± .14	.19 ± .01
810911-02	M	B	14.70 ± .25	1.71 ± .11	5.37 ± .10	10.11 ± .55	14.30 ± .35
		F+P		.630 ± .03	1.75 ± .16	.750 ± .14	.53 ± .08
		$\overline{B}$	24.27 ±11.17	1.65 ± .06	4.81 ± .53	10.00 ± .79	15.16 ± .75
		$\overline{F+P}$		.689 ± 1.79	1.38 ± .32	1.03 ± .47	.79 ± .76

Bananaquit

Individual	Sex	Tissue Type	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
801110-01	M	B	45.91 ± .99	1.78 ± .04	5.22 ± .13	6.47 ± .63	13.15 ± .60
		F+P					
801216-01	M	B	39.66 ± 1.67	1.51 ± .01	4.52 ± .02	7.73 ± .46	13.96 ± .58
		F+P		.692 ± .01	1.18 ± .10	1.30 ± .10	<1
810430-04	M	B					
		F+P					
810806-01	M	B					
		F+P					
810910-10	M	B					
		F+P					
810911-05	M	B					
		F+P					
		$\overline{B}$	42.79 ±	1.65 ± .14	4.87 ± .35	7.10 ± .63	13.56 ± .40
		$\overline{F+P}$		.692 ± .01	1.18 ± .1		

Puerto Rican Tanager

Individual	Sex	Tissue Type	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	Ash
801215-01	M	B					
		F+P					
801215-02	-	B	13.26 ± 2.56	1.67 ± .07	5.67 ± .19	9.28 ± .25	14.36 ± .38
		F+P		.692 ± .04	1.26 ± .02	1.06 ± .09	1
801215-03	M	B	18.61 ± 3.28	1.54 ± .28	5.27 ± .19	7.56 ± .23	11.64 ± 1.12
		F+P		.799 ± .01	1.09 ± .01	1.01 ± .06	<1
810317-01	F	B					
		F+P		.577 ± .01	1.34 ± .05	.622 ± .05	<1
810317-02	F	B					
		F+P					
810317-03	F	B	25.00 ± .87	1.60 ± .03	5.49 ± .26	7.26 ± .09	13.28 ± 1.26
		F+P		.610 ± .04	1.36 ± .04	1.11 ± .09	.77 ± .07
810413-04	M	B					
		F+P					
		$\overline{B}$	18.95 ± 5.87	1.60 ± .07	5.48 ± .20	8.05 ± 1.09	13.09 ± 1.12
		$\overline{F+P}$		.670 ± .10	1.26 ± .12	.961 ± .18	<1

Individual	Sex	Tissue Type	Ca⁺⁺	Mg⁺⁺	Na⁺	K⁺	Ash
			Puerto Rican Emerald				
801027-01	M	B F+P					
801029-01	F	B F+P					
801111-01	F	B F+P					
801118-01	F	B F+P					
810318-53	M	B F+P					
810318-54	M	B F+P					
810318-61	M	B F+P					
				.909 ± .06	2.51 ± .13	2.33 ± .92	1.56 ± .05
			B.W. Vireo				
810413-05	M	B F+P					
810426-01	F	B F+P					
			Puerto Rican Bullfinch				
810310-01		B F+P					
comb. birds		$\overline{B}$ $\overline{F+P}$	28.29 ± 8.46 .91	1.64 ± .07 .629 ± .09	4.87 ± .49 1.31 ± .11	8.08 ± 1.06 .982 ± .17	13.68 ± .97 1.80 ± .77

Calcium was the most abundant inorganic ion in the ash, being an average of 3.5 times the amount contributed by Mg^{++}, Na^{+}, and K^{+} combined. At approximately 40 mg/g this was true of all groups except birds whose average content was much lower, near 30 mg/g dry weight. This is consistent with their need for a light skeleton in order to achieve flight. Bats on the other hand, averaged 43 mg/g. Calcium was present in feathers below the detection level of our assay, but in special tests conducted, the content was estimated to be around 1 mg/g dry weight.

Potassium, sodium and magnesium averaged 7.5, 6.0, and 1.9 mg/g respectively, but again these values were lower for bird samples. It was not unusual that feathers, being mostly keratin, contained 0.38, 0.27, and 0.12 as much Mg^{++}, Na^{+}, and K^{+}, respectively, as their body counterparts.

The average amount of nitrogen for all species studied was between 19 and 23%. The protein nature of the feathers justified their somewhat higher value of approximately 26%. Sturges _et al._ (1974) reported much lower values for nitrogen from whole birds collected at Hubbard Brook. Their values were roughly one order of magnitude smaller than those presented here. However, on the other hand, our values for ripe fruit from the genus _Ficus_ are in agreement with those of Milton and Ditznis (1981). This confirms, at least in part, the precision of our assay and is evidence for the accuracy of our data.

Phosphorus averaged 4.5% for all species. In feathers this element was nearly 30 times less, around 0.16% of their dry weight.

Sulphur values varied between 0.6 and 1%, but the average of all species combined was approximately 0.75 percent. (Frogs were an exception as they averaged only 0.26%). The reason for this is not known. Feathers had slightly over twice as much sulphur as tissue. This is consistent with the presence of disulphide links for the structural integrity of keratin fibrile.

5.2.2 Calorimetry

The caloric value of all materials analyzed remained around 5,000 cal/g. Bird data except for nitrogen are still incomplete. Trends seem to indicate that average figures will not differ significantly from the few values collected thus far.

Using population data from Table 7 (Woolbright and Reagan, unpub. data), the amounts of the various elements were calculated on a per hectare basis. Results are shown in Table 8 for lizards and frogs. Not evident from these data is that population density is more important in determining the standing crop value than average elemental content of a species. This was true for each of the parameters determined.

5.3 Vegetation Studies

Considerable information has been gathered on the vegetation of the Luquillo mountains in Puerto Rico. Britton and Wilson (1923-1930), Wadsworth (1951), White (1963), Little and Wadsworth (1964), Odum and Pigeon (1970), Little and Woodbury (1976), Crow and Weaver (1977), Crow (1980), and Brown _et al_. (1981) are some of the most important contributors. Of the many studies, summaries and surveys, no one had previously conducted a within forest type (tabonuco) variability study of the vegetation.

Variation in structure and function in a forest is mainly related to the physical environment (water and energy regimes) and its effects on soils and topography (Brunig and Klinge 1975). However, variability must be analyzed at different levels of organization. At the species level, water, light, soil and topographical diversity may determine variations in composition and rates of productivity. At the ecosystem level, the same forest and abiotic inputs function together as a unit.

A measurement of the tabonuco forest variability was essential in order to detect organizational levels as well as yield baseline data for future comparisions among other natural forests and plantations. The present studies were designed, therefore, to measure and compare

Table 7. Population densities and weights of amphibians, reptiles and bats.

Species	Population Densities		
	Individuals/ha.	Average Individual Weight in g	
		Wet	Dry
Eleutherodactylus coqui	22,000	2.86	.53
Anolis evermanni	2,000*	2.94	.71
Anolis gundlachi	2,000	3.60	.86
Anolis stratulus	25,000	2.13	.51
Artibeus jamaicensis	N.D.	41.11	14.47

Average individual weight comprises males, females and juveniles.

*Uppermost limit of estimate.

Table 8. Elemental standing crops of amphibians and reptiles.

	Elemental Standing Crops g/ha.							
Species	Ca^{++}	Mg^{++}	Na^{+}	K^{+}	N	P	S	Total energy kcal/ha.
Eleutherodactylus coqui	461	23	74	86	2,718	457	30	50,633
Anolis evermanni	55	2.8	8.2	13	299	62	10.9	6,270
A. gundlachi	86	3.6	11.8	11.3	477	79.5	16	7,466
A. stratulus	384	23.6	75	98	2,320	537	111	69,634

variability of each and all species storages and flows among and, in some cases, within four 1 ha randomly selected plots.

5.3.1 Plot Characteristics

Minimal Area

The minimal area curves constructed for El Verde on the design of Mueller-Dombois and Ellenberg (1974) indicated that a plot size of 2150 m^2 would yield $\leq$10 percent increase in the number of new plant species (Figure 5). A plot area of 3400 m^2 would yield a $\leq$ 5 percent increase in the number of new species (Figure 6).

An area of 1 ha (10,000 m^2) was selected as the size of each of the four plots. This larger size was considered to be more than adequate in earlier studies at El Verde (Smith 1970). One ha would also assure valid results with multiple plot usage.

Structural Analysis

The tabonuco forest basal area of live trees $\geq$ 10cm dbh (a mean of the four study sites) was 30.75 m^2/ha. This value is within the range (17-50 m^2/ha) reported by Soriano-Ressy et al. (1970) and Odum (1970) and close to the 35.7 m^2/ha value Crow (1980) reported for stems $\geq$4 cm dbh in this area. A nearby 40 year old multi-species natural succession stand had a basal area of 27.9 m^2/ha; a 40 year old plantation of Calophyllum calaba, 30.2 m^2/ha; and a 17 year old plantation of Pinus caribaea, 33.9 m^2/ha (Jordan and Farnworth unpublished data). However, a similar tabonuco forest site on the island of Dominica, British West Indies, had basal areas of 90.5 - 130.9 m^2/ha (Soriano-Ressy et al. 1970). The basal areas of the Dominica sites are probably representative of the structural potential of a completely undisturbed tabonuco forest.

Individual plot live tree basal area data are given in Table 9. Values less than 30 m^2/ha in the Odum (1970) studies were generally from cutover or disturbed sites. Judged by species composition and canopy cover, plot 4 is disturbed. The basal area of plot 4 (24.8

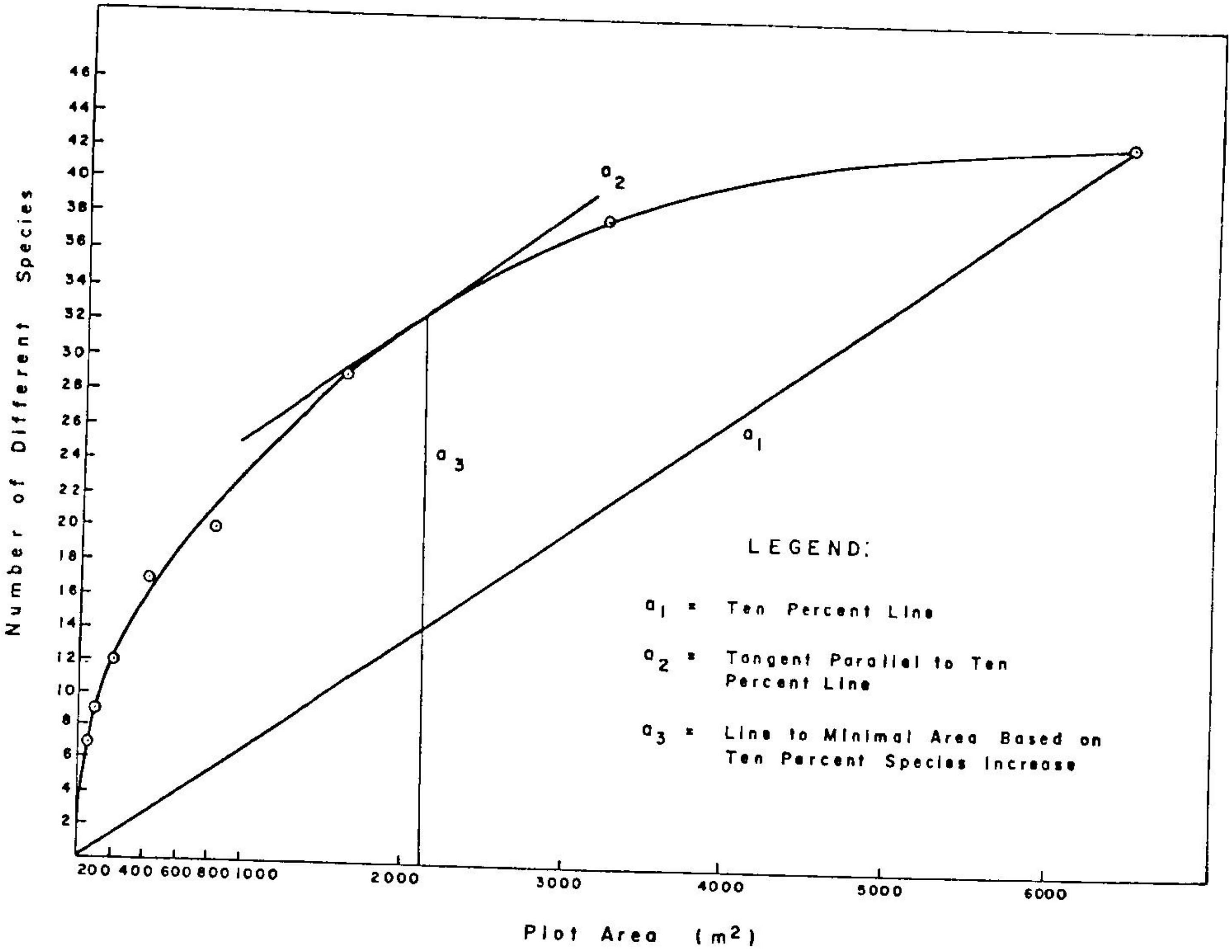


Figure 5. Minimal area curve for El Verde (10%).

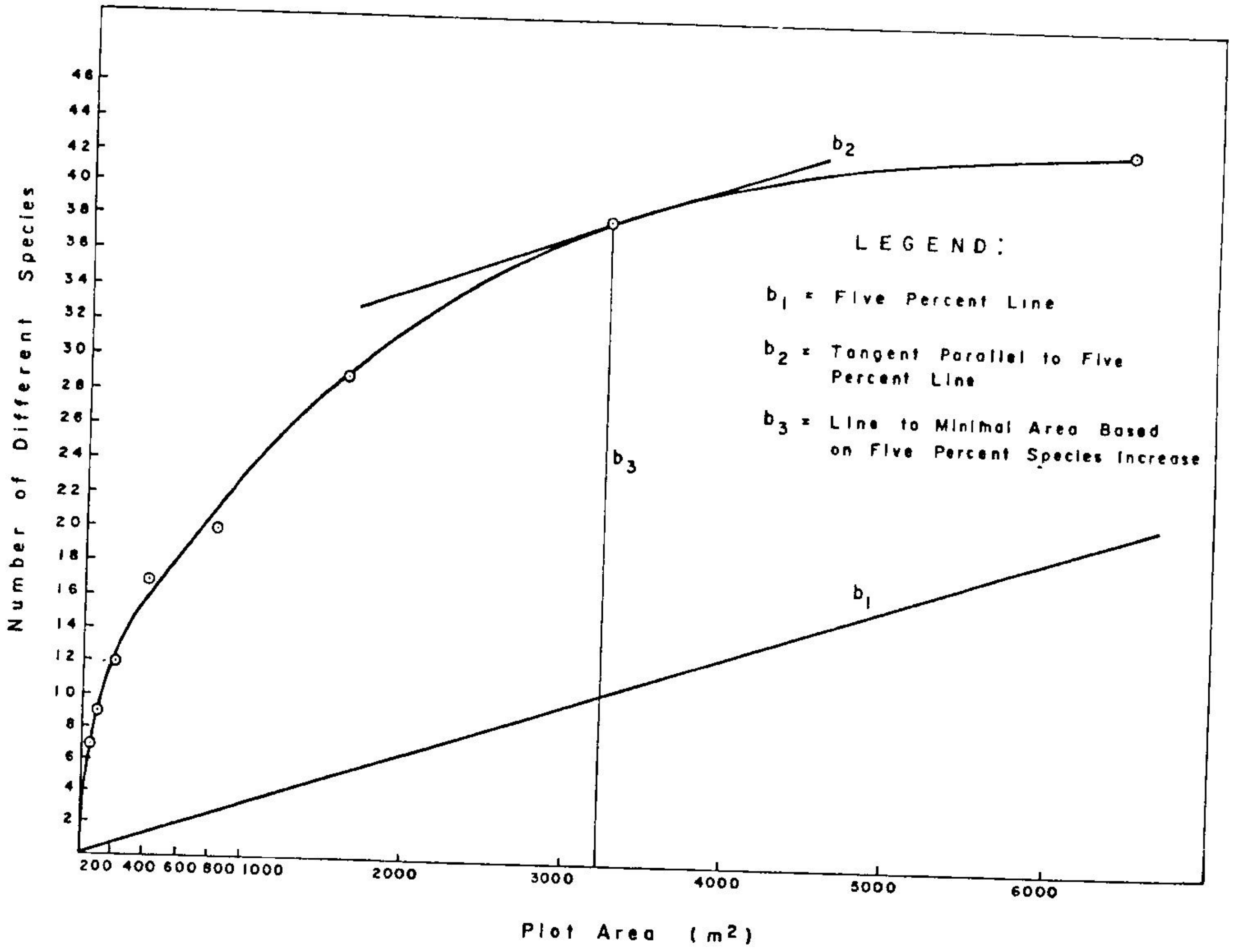


Figure 6. Minimal area curve for El Verde (5%).

Table 9. Basal area (B.A.), density (Ind./ha) and importance values (I.V.) of ten most significant species of trees among four plots.

Species	Plot 1 BA m^2/ha	Plot 1 Ind./ha	Plot 1 I.V.	Plot 2 BA m^2/ha	Plot 2 Ind./ha	Plot 2 I.V.	Plot 3 BA m^2/ha	Plot 3 Ind./ha	Plot 3 I.V.	Plot 4 BA m^2/ha	Plot 4 Ind./ha	Plot 4 I.V.
Prm	4.7	261	61	6.4	299	84	2.5	145	36	1.4	83	35
De	4.4	89	35	2.4	70	29	5.8	108	41	0.9	19	13
Cp	4.3	115	38				1.1	51	13			
Ok	3.3	19	15	1.1	13	9				1.1	6	7
Sb	2.6	51	21	3.5	45	33	2.8	83	28			
Mg	2.1	19	11									
Hor	1.4	6	6	1.0	6	5	2.6	19	28			
Sl	1.4	32	12									
Ns	1.4	13	8									
Dm	1.1	6	5									
Gt							5.1	38	4			
Bc				1.8	13	11	3.0	19	14	2.2	6	12
Mb							1.7	64	21			
Cep							1.6	26	12	3.3	32	27
Ifa				5.4	76	39	1.3	32	11	3.2	19	22
Th				1.7	19	13						
Ap				3.4	38	24						
Mys				1.0	38	12						
Ca										5.2	166	76
Zm										1.3	13	11
Ol										1.0	26	15
Da										0.8	19	12
Total	26.7	611	212	27.7	617	259	27.5	585	208	20.5	389	230
% of total live species	81	72	71	90	83	86	80	72	69	82	76	77
Total live	33.0	847	300	30.9	739	300	34.3	816	300	24.8	515	300
Total dead	2.9	45		1.4	32		1.5	57		2.8	38	

m^2/ha) supports this premise. Plots 1 and 3 with basal areas of 33.0 and 34.3 m^2/ha respectively, fall within the range represented in Puerto Rico as a mature forest.

Mean density of the study site trees was 729 ind/ha. Wadsworth (1951) reported 655 ind/ha in his measurement of a virgin tabonuco forest near El Verde. The densities of plots 1-4 (Table 9), were 847, 739, 816, and 515 ind/ha, respectively. White (1963) indicated an increase of density with elevation. However, the 150 m elevation differences among plots cannot account for the differences in density. In plot 4, the disturbed site, the lower density is probably representative of selective cutting known to have occurred there (Crow 1980).

Twenty-three families of tree species were represented in the four 1 ha plots (Table 10). Of these families, 14 were represented by the dominants of the plots. The greatest number of species (5) were from the Euphorbiaceae; the greatest basal area (4.3 m^2/ha) in the Leguminosae; and the greatest density (197 ind/ha) in the Palmae.

There are 547 native tree species found in Puerto Rico (Little and Wadsworth 1964). Two hundred twenty-five species are found in the Caribbean National Forest (Little and Woodbury 1976). Sixty-five species were found by Wadsworth (1951) in 25 ha of the same tabonuco forest type. In this 4 ha study, 44 species were found.

Variation in forest structure among the four plots is shown in Table 9. The dominant species in each plot (determined by largest basal area) are listed by basal area, density and importance value (relative dominance + relative density + relative frequency = importance value; Cottam and Curtis 1956). Two species, Dacryodes excelsa (tabonuco) and Prestoea montana (sierra palm) were dominant in all four plots; five (Bc, Hor, Ifa, Ok and Sb; see Table II for species symbol key) in three plots; two (Cp and Cep) in two plots; and thirteen (ap. Ca, Da, Dm, Gt, Mb, Mg, Mys, Ns, Ol, Sl, Th, and Zm) in one plot. The dominant species at each site represented 80-90 percent of the basal area, 72-83 percent of the density, and 69-86 percent of the species importance. The remaining 22 species comprised the rest of the forest.

Table 10. List of species in each family including average basal areal (BAm^2/ha) and density (Ind/ha) for each family.

Family	Species	Family BAm^2/ha	Family Ind/ha
Leguminosae	Ai, Ifa, Iv, Ok	4.3	54
Palmae	Prm	3.8	197
Euphorbiaceae	Al, Ap, Cp, Dg, Sl	3.7	97
Burseraceae	De, Tb	3.5	75
Flacourtiaceae	Ca, Cbi, Cs, Hor	3.2	75
Elaeocarpaceae	Sb	2.2	45
Combretaceae	Bc	1.8	10
Meliaceae	Gt	1.4	13
Sapotaceae	Mb, Mg, Mic	1.3	37
Lauraceae	Bp, Ns, Ol, Om	1.2	21
Moriaceae	Cep	1.2	10
Araliaceae	Da, Dm	1.0	18
Bignoniaceae	Th	0.6	10
Melastromataceae	Csg, Mt	0.4	16
Myrtaceae	Es, Myd, Mys	0.4	16
Rutaceae	Zm	0.3	3
Annonaceae	Oka, Okl	0.1	8
Boraginaceae	Csl	0.1	6
Oleaceae	Ld	0.1	3
Sapindaceae	Md	0.1	2
Nyctaginaceae	Pia	0.04	2
Polygonaceae	Cos	0.02	2
Rubiaceae	Gl	0.02	2

Table 11. Species symbols and corresponding scientific names for trees.

Species symbol	Scientific name
Ai	*Andira inermis*
Al	*Alchornea latifolia*
Ap	*Alchorneopsis portoricensis*
Bc	*Buchenavia capitata*
Ca	*Casearia arborea*
Cbi	*Casearia bicolor*
Cep	*Cecropia peltata*
Cos	*Coccoloba swartzii*
Cp	*Croton poecilanthus*
Cr	*Cyrilla racemiflora*
Cs	*Casearia sylvestris*
Csl	*Cordia sulcata*
Csg	*Calycogonium squamulosum*
Da	*Dendropanax arboreus*
De	*Dacryodes excelsa*
Dg	*Drypetes glauca*
Dm	*Didymopanax morototoni*
Es	*Eugenia stahlii*
Gl	*Guettarda laevis*
Gt	*Guarea trichilioides*
Hor	*Homalium racemosum*
Ifa	*Inga fagifolia*
Iv	*Inga vera*
Ld	*Linociera domingensis*
Mb	*Manilkara bidentata*
Md	*Matayba domingensis*
Mg	*Micropholis garciniaefolia*
Mic	*Micropholis chrysophylloides*
Myd	*Myrcia deflexa*
Mys	*Myrcia splendens*
Ns	*Nectandra sintenisii*

Continued table 11.

Species symbol	Scientific name
Ok	Ormosia krugii
Oka	Oxandra laurifolia
Okl	Oxandra lanceolata
Ol	Ocotea leucoxylon
Om	Ocotea moschata
Pia	Pisonia albida
Prm	Prestoea montana
Rg	Rourea glabra
Sb	Sloanea berteriana
Sl	Sapium laurocerasus
Tb	Tetragastris balsamifera
Th	Tabebuia heterophylla
Zm	Zanthoxylum martinicense

With regard to similarities and differences, plots 1 and 3 are most similar in basal areas and densities; plot 4, the most different. All plots are dominated by the tabonuco and the sierra palm, even though species composition is different. The proportion of basal area, density and importance of the dominants in each plot is similar although the dominant species are different. These differences are probably the result of microclimatic and microtopographical plot variability.

5.3.2 Phenology

Phenology of the trees in the tabonuco forest in El Verde was extensively studied by Estrada (1970) from 1963 to 1967. Since flowers and/or fruits were expected to be an important energy source in the current faunal food web studies, among plot and species phenological patterns occurring during the study were sampled using materials collected in the litter fall baskets.

Fruits contributed twice as much to litter fall as flowers with values of 29.9 to 14.4 $g/m^2.yr$, respective (Table 12). The greatest fruitfall was in January (5.6 g/m^2); flower fall in July (2.8 g/m^2). Fruits consisted of 3.9 percent of the total yearly litterfall; flowers, 2.0 percent. The individual species input to the flower and fruit fall has yet to be analyzed.

5.3.3 Litter Fall

The return of litter to the soil (litter fall) is an important nutrient cycling mechanism (Ewel 1976). Jordan (1970) states from a study conducted in El Verde that litter fall is a relatively unimportant nutrient transfer mechanism as compared to throughfall and stemflow. Jordan corrected his calculation in Brown et al. (1981) and now concurs with Ewel. Due to its importance, litter fall was measured on a bimonthly basis to detect between site and species variability.

Similarities at an ecosystem level and differences at a species level are most apparent in the leaf fall component of litter fall. A five year monthly mean is shown in Figure 7. The month-to-month

Table 12. Mean monthly litter fall values (g/m^2) by categories for 1981.

Months	Leaves	Flowers	Fruits	Wood	Miscellaneous	Total
J	23.5	0.7	5.6	8.0	9.0	46.6
F	24.3	0.4	2.4	9.9	11.7	48.6
M	57.5	0.7	1.4	13.8	15.4	88.7
A	41.0	0.4	2.1	13.6	16.0	72.9
M	81.8	0.3	1.1	18.0	22.4	123.4
J	37.1	1.0	1.3	7.2	19.1	65.7
J	45.7	2.8	2.1	8.9	17.0	76.3
A	36.6	1.9	3.3	17.0	19.2	77.8
S	47.9	1.0	1.6	39.3	27.0	116.7
O	42.8	1.6	3.0	5.0	8.6	60.7
N	31.5	2.4	3.6	6.4	5.8	49.6
D	21.9	1.2	2.4	9.0	9.0	43.2
Mean	491.4	14.4	29.9	156.1	180.2	870.2

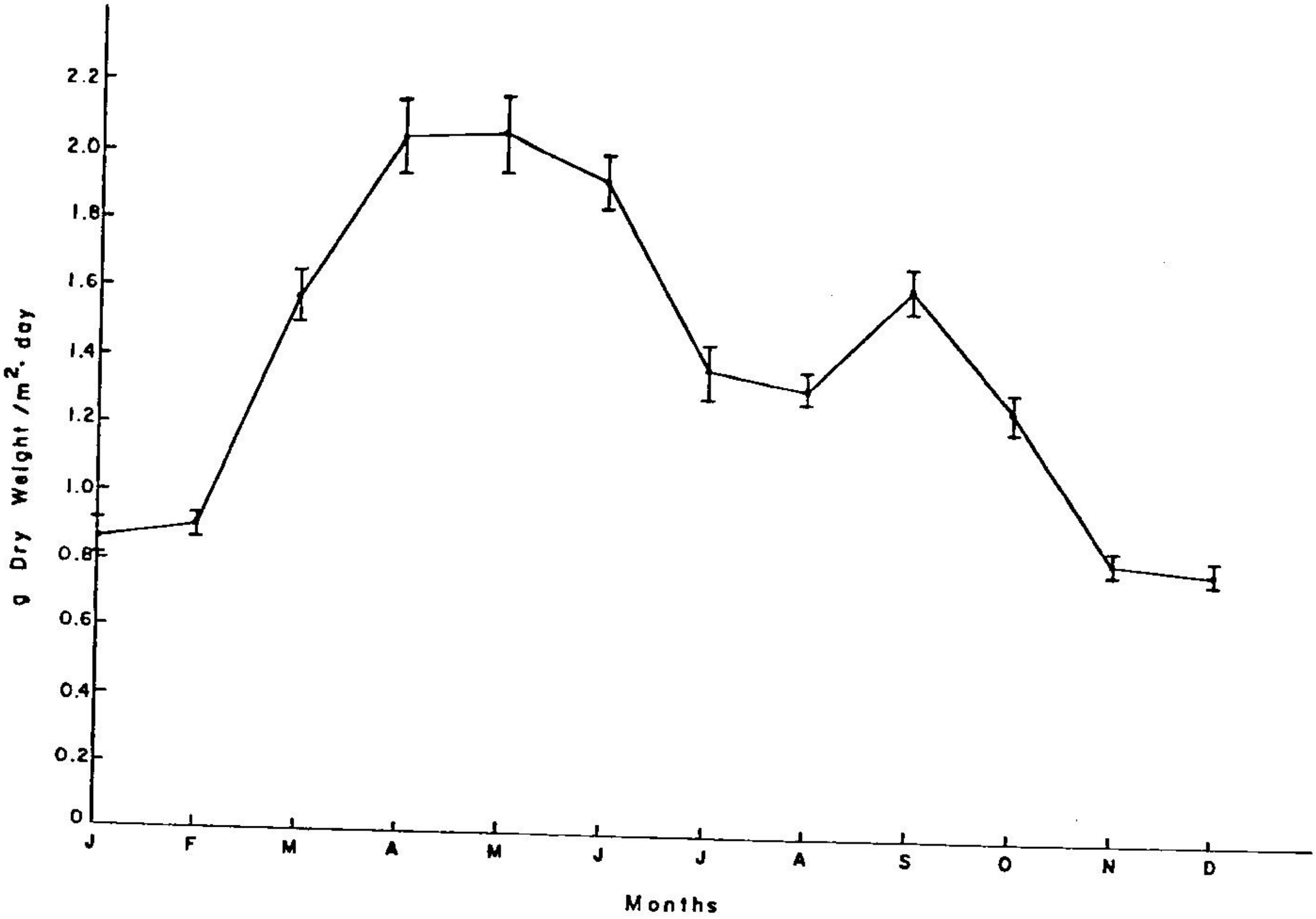


Figure 7. Five year mean leaf fall plus or minus one standard error.

variations during the 5 yrs. are shown in Table 13 (1970-73 from Estrada, unpublished data plus this year). An analysis of variance (Table 14) indicated no significant difference ($p > .05$) among years. However, differences were highly significant ($p < .001$) among months but there were no significant differences among plots.

The 1.39 g/m^2 day value obtained from the 5 yr leaf fall mean was similar to the 1965-1966 mean leaf fall input of 1.43 g/m^2 day in a study conducted by Weigert (1970) in El Verde. Thus, in spite of a span of 18 years and site and species composition differences, the tabonuco forest type consistently cycles the same amount (g/m^2) of leaves annually from trees to forest floor; the tabonuco forest is functioning as a mature ecosystem with respect to leaf fall.

Similar biotic and climatic regimes should exhibit similar leaf fall inputs. Table 15 illustrates the effects of general climatic conditions on the rate of leaf fall, demonstrating the trend that leaf fall decreases with increasing latitude (Jordan 1971). The El Verde value of 5.1 mt/ha/yr corresponds to other sub-tropical forest leaf fall studies.

Bray and Gorham (1964) show variable yearly litterfall input in temperate, less diverse forests. Since in our study six years of leaf fall measurements yielded no significant differences, variation of leaf fall yearly inputs may be buffered by high species diversity in the tropical forests. However, a six-year sub-tropical mangrove litter fall study (Lugo _et al_. 1980) with two species varied less than 11 percent among annual means. A favorable climate may be more important for consistent litter production than species diversity.

The four plot monthly mean litter fall components are in Table 12. These inputs are represented as a percent of total in Table 16 and graphically in Figure 8. Bray and Gorham (1964) report a mean value in which 33 percent of non-leaf litter was found in litter fall from a tropical forest. In addition, 16 percent of total litter fall consisted of wood and 20.8 percent miscellaneous (unidentifiable) material. The greatest amount of wood and miscellaneous material input occurred during September as the result of high winds from a tropical storm.

Table 13. Mean monthly leaf-fall of four plots in g/m^2 for 5 years including the 5 year mean. Yearly totals and rates in g/m^2 day are also given.

Month	1970	1971	1972	1973	1981	5 yr. mean
			YEAR			
J	22.1	30.1	26.7	30.3	23.5	26.5
F	24.9	22.7	29.8	24.9	24.3	25.3
M	74.1	43.7	32.9	36.2	57.5	48.9
A	43.7	77.4	59.3	86.5	41.0	61.6
M	46.9	67.5	48.9	75.7	81.8	64.2
J	80.5	57.6	59.6	55.2	37.1	58.0
J	45.0	45.1	46.7	31.5	45.7	42.8
A	44.5	40.7	45.8	38.2	36.6	41.2
S	43.6	54.2	32.8	64.1	47.9	48.5
O	49.7	44.1	30.4	30.1	42.8	39.4
N	25.8	18.5	27.5	20.5	31.5	24.8
D	32.0	29.3	22.6	17.5	21.9	24.7
Yearly total	532.8	530.9	463.0	510.7	491.6	505.9
g/m^2 day	1.46	1.45	1.27	1.40	1.35	1.39

Table 14. One way analysis of variance among litter fall and leaf fall in 1981. F values demonstrate significance among plots, months and years.

	Litter fall	Leaf fall
Among 4 plots	0.10^{ns}	0.19^{ns}
Among 12 mos.	19.3^{***}	14.5^{***}
Among 5 years	not available	0.22^{ns}

ns = $p > .05$

*** = $p < .001$

Table 15. Comparison of cycling and storage components by latitude.

Location	Litter Fall mt/ha	Leaf Fall mt/ha	Ground Litter mt/ha	TOR	Decomposition years to total	Decomposition %/day	Forest type	Author(s)
TROPICAL								
Panama		7.0		2.6			mean	Swift et. al., 1977
Panama	11.3		6.2	1.8			moist	Golley, et. al., 1975
Panama	10.4		4.8	2.2			wet	Golley, et. al., 1975
Brazil	21.0							Stark, 1971
Brazil	7.3	5.6						Fittkaw and Klinge, 1973
Trinidad		7.0	4.0			0.45		Cornforth, 1970
Nigeria		4.7	1.0	4.5	0.2		moist	Hopkins, 1966
Nigeria		4.5	2.4	1.9	0.5		moist	Hopkins, 1966
Nigeria		7.1	3.0	2.4	0.4		moist-ever-green	Hopkins, 1966
Ghana	10.6	7.0	2.3			1.3		Nye, 1961
Panama	11.1	5.8						Haines and Foster, 1977
Panama	11.4	6.6						Leigh, 1975
Worldwide	9.6	7.1					(rain, wet, moist)	Brown & Lugo,1982
Colombia	10.0		10				mean	Jenny et. al., 1949
Worldwide	10.9	6.8					mean	Bray and Gorham, 1964
MEAN	11.4	6.3	4.2	2.6	0.4	0.9		
SUB-TROPICAL								
Florida	7.3	5.5	3.8	1.9	0.5		mangrove	Lugo et. al., 1981
Puerto Rico	8.7	5.1	3.9	1.8	0.5		wet	This study
Puerto Rico		5.3	5.9				wet	Weigert, 1970
Worldwide	7.2	5.4					(rain, wet, moist)	Brown & Lugo, 1982
Jamaica					0.9		lower montane rain	Grubb, 1977
Jamaica					0.5		Upper montane rain	Grubb, 1977
MEAN	7.7	5.3	4.5	1.9	0.6			
TEMPERATE								
Worldwide	5.3	3.2					mean	Swift, et. al., 1979
New Hampshire		2.9						Leigh, 1975
California	2.0		63					Jenny et. al., 1949
Worldwide	3.5	2.5						Bray and Gorham, 1964
MEAN	3.6	2.9	63					
ARTIC ALPINE								
Worldwide	1.0	0.7						Bray and Gorham, 1964

Table 16. Components of litter fall (in per cent) expressed as means of four plots in 1981. The standard error is in parenthesis.

Month	Leaves	Flower	Fruit	Wood	Miscellaneous
J	52.0 (5.4)	1.5 (0.7)	10.8 (3.7)	16.9 (6.0)	18.6 (4.0)
F	51.6 (1.2)	1.1 (0.6)	4.0 (1.3)	17.1 (3.2)	25.9 (3.1)
M	66.3 (3.6)	0.9 (0.4)	1.4 (0.7)	15.0 (1.8)	16.3 (2.3)
A	56.1 (2.7)	0.5 (0.4)	2.6 (1.7)	19.9 (2.5)	20.4 (3.7)
M	65.5 (7.5)	0.3 (0.3)	0.6 (0.3)	14.9 (3.3)	18.6 (4.5)
J	56.6 (1.8)	1.5 (0.6)	1.9 (0.5)	11.0 (0.7)	29.1 (2.4)
J	60.1 (2.9)	3.6 (2.0)	2.8 (0.7)	12.3 (1.3)	21.3 (2.4)
A	47.5 (2.0)	2.9 (0.8)	3.5 (1.2)	18.3 (3.3)	28.3 (3.9)
S	44.9 (4.4)	1.5 (0.5)	2.1 (0.5)	23.9 (7.5)	28.4 (4.7)
O	71.1 (1.9)	3.5 ((0.7)	5.0 (1.7)	9.6 (0.1)	11.6 (1.1)
N	64.0 (0.3)	4.8 (1.7)	7.6 (1.1)	13.0 (1.6)	11.1 (3.9)
D	52.2 (2.9)	2.6 (0.9)	5.4 (1.2)	19.6 (3.8)	20.8 (2.2)
Mean	57.3 (1.3)	2.0 (0.3)	3.9 (0.5)	16.0 (1.0)	20.8 (1.1)

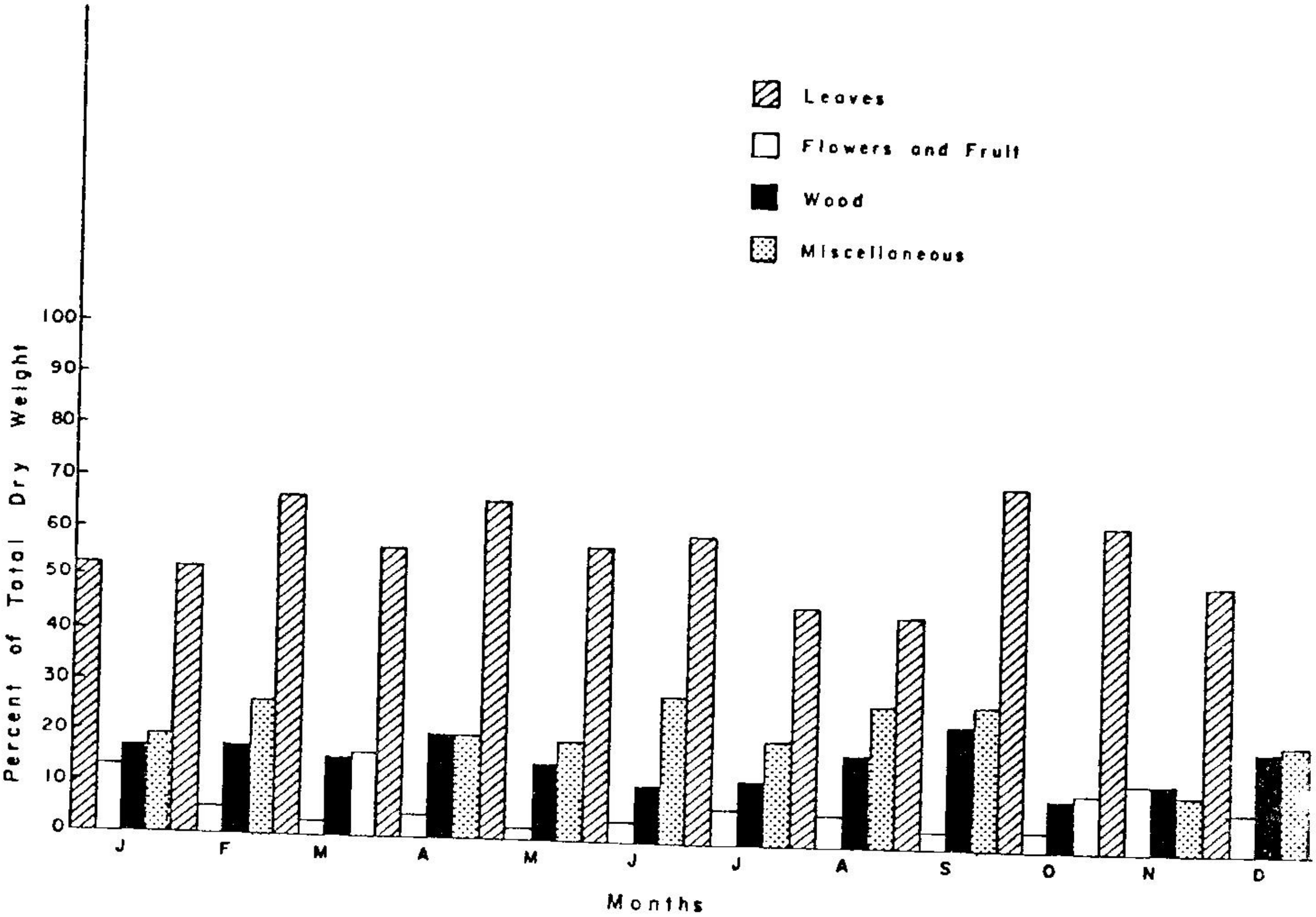


Figure 8. Components of litter fall (means of four plots).

Rainfall data are in Table 17. A linear regression comparing litter fall to rainfall showed little correlation (r^2=0.16). Leaf fall cannot be associated with wind speed, day length, or moisture alone but more likely to a combination of environmental factors (Hopkins 1966).

Differences in leaf fall are most notable at the species level (Table 18-19). Values are given by plot for the 15 species that contributed the greatest amount to the leaf fall component. Plot A refers to collections from 1973 (Estrada, unpublished data). Although leaf fall input does not significantly differ among plots, the amount that each species contributes varies significantly. Apparently the input or lack of it by one species is compensated by another species in a diverse system.

Plot 4 yielded the greatest leaf fall input. If leaf fall is a measure of net primary productivity (Murphy 1977), plot 4 is the most productive. Yet plot 4 exhibited the lowest basal area and density of all plots and is considered to be the earliest successional stage of the four plots. In Ewel's (1976) study of tropical forests in Guatemala, litter fall from a successional 14 yr old stand did not significantly differ from a mature forest. In some cases, litter fall in successional areas is greater than mature forests. Apparently the energy obtaining component (leaves) receives greatest priority in a successional system. The rapid growth of vines, shrubs, and short-lived trees compensates for the original plant production while the forest slowly rebuilds.

5.3.4 Loose Litter

Litter standing crop constitutes the ground storage of plant parts during the decomposition process when plant organic matter is converted to soil organic matter or mineralized. Loose litter builds up during the successional process until litter fall is balanced by decomposition (Ewel 1976). In a mature forest, loose litter is at equilibrium.

Litter standing crop generally varies inversely to litter fall at

Table 17. Rainfall in mm from El Verde, P.R., during the litterfall study period.

Months			Year			Mean	Mean
	1970	1971	1972	1973	1981	4 yr.	15 yr.
J	446.5	304.3	254.3		216.6	305.4	249.5
F	109.2	277.1	181.4		233.1	200.2	193.8
M	74.7	102.0	170.2	NOT AVAILABLE	287.9	158.7	169.9
A	80.8	119.4	156.5		539.0	223.3	225.2
M	325.6	183.6	115.6		551.2	294.0	397.4
J	507.5	90.2	140.7		234.2	243.2	236.4
J	445.0	172.7	178.8		447.5	311.0	271.0
A	323.8	223.3	217.2		402.8	291.8	339.7
S	208.0	197.0	188.5		194.6	197.0	307.7
O	545.1	328.6	202.4		238.4	328.6	369.0
N	346.2	208.8	158.2		189.8	225.8	382.9
D	511.0	405.9	222.0		337.0	369.0	360.0
Yearly total (mm)	3923.4	2612.9	2185.5		3872.1	3148.0	3502.5
Yearly total (in)	154.5	102.0	86		152	123.9	137.9

Table 18. Mean leaf fall input (g/m^2. year) by species illustrating between plot variability and mean contribution to total forest. Plot A refers to the 1973 collection while plots 1-4 demonstrate input during 1981.

	g/m^2 year					Mean	
Species	Plot A	Plot 1	Plot 2	Plot 3	Plot 4	g/m^2 year	% of total
De	69.9	107.9	78.0	112.3	21.2	77.9	16
Bc	35.3	3.5	63.1	46.7	117.7	53.3	11
Ca	0.0	13.6	8.8	9.9	102.4	26.9	5
Ifa	10.0	8.3	64.1	10.3	20.3	22.6	5
Ok	25.8	23.0	38.4	4.8	4.1	19.2	4
Mb	18.0	22.6	0.0	40.6	10.6	18.4	4
Gt	0.0	0.4	6.0	66.3	14.7	17.5	4
Cep	0.7	1.9	24.7	20.2	35.3	16.6	3
Hor	5.2	14.2	29.2	30.7	0.0	15.9	3
Sb	6.4	36.8	9.8	24.8	1.1	15.8	3
Rg	41.4	3.5	3.9	15.7	9.3	14.8	3
Prm	0.0	21.9	29.6	0.0	20.5	14.4	3
Cr	68.3	0.0	0.0	0.0	0.0	13.7	3
Md	55.6	5.5	2.0	1.7	0.0	13.0	3
Cp	13.2	45.0	0.0	4.8	0.0	12.6	3
81 other species						141.0	29
Total	502.5	451.4	491.9	509.3	512.8	493.6	

Table 19. 1981 mean leaf fall (g/m^2) values from four plots for 10 species of trees.

Species	J	F	M	A	M	J	J	A	S	O	N	D
De	1.9	1.6	4.2	9.4	11.0	7.2	27.5	2.7	3.6	3.6	3.0	2.2
Bc	2.8	3.4	13.5	8.3	8.2	1.7	1.6	2.0	3.4	2.5	3.6	2.3
Ca	1.1	0.9	3.1	1.9	3.9	2.6	3.3	1.8	3.4	1.9	2.1	0.9
Ifa	0.9	0.5	2.3	1.0	1.4	4.5	1.4	1.3	3.5	1.8	2.1	1.9
Ok	0.4	0.8	2.9	1.9	2.0	1.7	2.0	2.1	1.5	1.7	1.2	1.0
Mb	0.9	0.3	2.4	1.2	1.6	2.5	2.6	1.2	0.7	2.4	1.6	1.0
Gt	0.4	0.3	1.4	2.0	2.0	0.5	1.1	1.7	2.0	3.0	2.2	0.9
Cep	0.3	1.1	2.1	2.2	2.3	1.1	1.2	1.0	1.5	1.2	2.0	0.6
Hor	0.4	0.5	1.0	3.2	9.6	0.0	0.2	0.0	0.5	0.6	0.7	0.0
Sb	1.1	0.4	2.3	1.2	2.1	1.7	1.2	0.6	1.2	1.7	1.1	1.2
Mean total for all species	23.5	24.3	57.5	41.0	81.8	37.1	45.7	36.6	47.9	42.8	31.5	21.9

increasing latitudes. Jenny et al. (1949) states that in a Colombian forest loose litter (1076 g/m^2) was one tenth loose litter in a Californian forest (11609 g/m^2) while litter fall in the Colombian site (1023 g/m^2) was five times the value from Californian (200 g/m^2). Table 15 gives comparative latitudinal litter storage values.

Jenny et al. (1949) calculated from litter fall rates and storage values that it would take a Colombian rain forest 1-3 years to reach equilibrium; California, 24-332 years depending on forest type (oak or pine) and altitude.

Ground litter storages in the four study plots in El Verde are shown in Figure 9 and Table 20 by category, site and season. The miscellaneous category consisted of all plant parts in all stages of decomposition except wood. The yearly mean ground litter storage was 392.2 g/m^2. This value is considerably lower than Weigert's (1970) El Verde mean of 598 g/m^2. We believe the four plot, two season mean of the current study (240 samples) is more reliable than Weigert's 1970 mean (100 samples). The present study's sampling design included greater representation of the tabonuco forest micro-topographical heterogeneity. Analysis of variance (Tables 21 and 22) demonstrated no significant variation in the miscellaneous category (leaf, flower and fruit component) among plots or between seasons. Greatest variability was in the wood component in two plots during the wet season. The lack of variability in the leaf fall and miscellaneous category of the ground litter indicates steady state.

Assuming equilibrium, annual input (leaf fall) can be divided by annual storage (loose litter) and the resulting turnover rate (TOR) of litter determined (Table 23). The four plot mean TOR was slightly faster during the wet season (1.90) than the dry season (1.68). A latitudinal comparison of TOR is given in Table 15.

TOR measures the rate of internal cycling within a forest and can represent decomposition. The mean TOR of 1.78 for El Verde would indicate complete decomposition of leaves within 0.56 years.

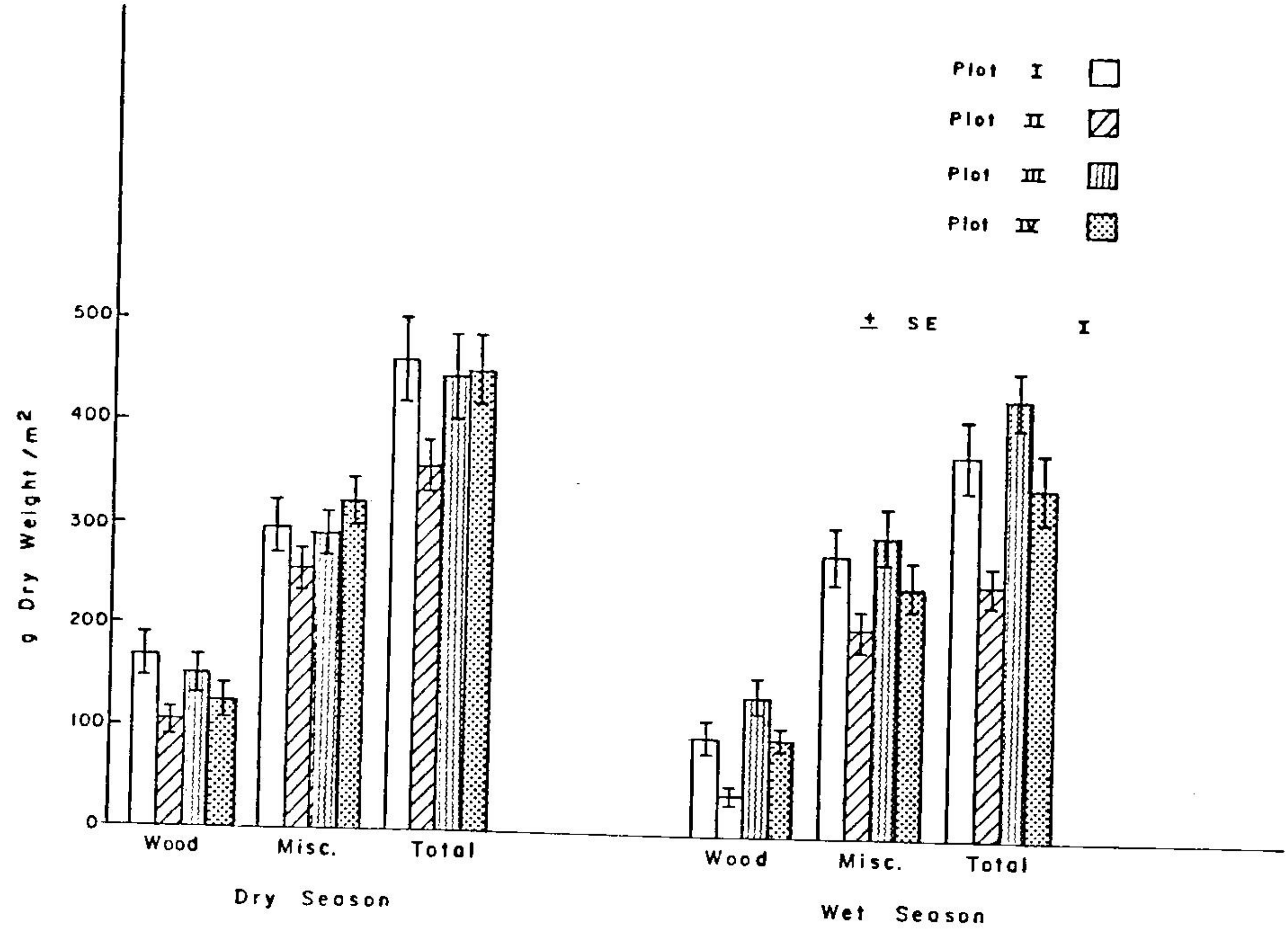


Figure 9. Loose litter components by plot and season.

Table 20. Plot and seasonal comparisons of mean loose litter values in g/m^2. The value in parenthesis represents the standard error.

	Dry Season			Wet Season		
	Wood	Miscellaneous	Total	Wood	Miscellaneous	Total
Plot I	169.0 (20.4)	295.7 (25.6)	464.8 (38.0)	98.7 (17.0)	278.3 (30.0)	377.0 (37.0)
Plot II	105.5 (13.9)	256.2 (19.5)	361.7 (26.5)	44.2 (8.6)	207.3 (18.3)	251.6 (19.7)
Plot III	151.5 (20.7)	293.6 (21.6)	445.2 (34.2)	137.6 (14.8)	299.9 (26.8)	437.5 (30.9)
Plot IV	126.2 (16.0)	326.9 (24.8)	453.1 (33.7)	96.9 (12.9)	249.4 (25.3)	346.0 (34.0)
Mean	138.0 (9.1)	293.2 (11.5)	431.2 (16.8)	94.4 (7.7)	258.8 (13.1)	353.2 (17.0)

Table 21. F values from one way analyses of variance of loose litter among plots at each season.

	Wood	Miscellaneous	Total	d.f.
Dry Season	2.41^{ns}	1.59^{ns}	2.00^{ns}	3,156
Wet Season	7.79***	2.47^{ns}	6.2***	3,76

ns = $p \geq .05$

*** = $p < .001$

Table 22 . F values from one way analyses of variance for loose litter between wet and dry seasons.

	Wood	Miscellaneous	Total	d.f.
Plot I	5.01*	0.17^{ns}	2.16^{ns}	1,58
Plot II	8.87**	2.56^{ns}	7.58**	1,58
Plot III	0.20^{ns}	0.03^{ns}	0.02^{ns}	1,58
Plot IV	1.43^{ns}	3.87^{ns}	3.99^{ns}	1,58
Combined plot comparison	9.74**	3.35^{ns}	8.6**	1,238

ns = $P > .05$

* = $P < .05$

** = $P < .01$

Table 23. Leaf fall and miscellaneous loose litter (kg/ha) and turn over rates (TOR = leaf fall/misc. loose litter) by plot and season.

	Plot 1	Plot 2	Plot 3	Plot 4	Mean
Dry Season					
Leaf fall	4514	4919	5093	5128	4914
Miscellaneous Loose litter	2956	2560	2936	3268	2932
TOR	1.53	1.92	1.73	1.57	1.68
Wet Season					
Leaf fall	4514	4919	5093	5128	4914
Miscellaenous Loose litter	2784	2072	3000	2496	2588
TOR	1.62	2.37	1.70	2.05	1.90
Yearly Mean					
Leaf fall	4514	4919	5093	5128	4914
Miscellaneous Loose litter	2870	2316	2963	2882	2760
TOR	1.57	2.12	1.72	1.78	1.78

5.3.5 Decomposition

Since weathering releases elements at too slow a rate to meet plant nutrient requirements, decomposition regulates the rate elements are returned to the system. decomposition either mineralizes litter storages (converts organic compounds to an inorganic useable form) or forms soil organic matter from the residue or both. The rate of decomposition regulates the net primary productivity of a system and the abiotic environment regulates decomposition (Swift et al. 1979(.

Decomposition rates are much slower in temperate climates than in the tropics (Table 15) and account for the increased litter standing crop and decreased TOR in temperate areas. Decomposition varies with species (Madge 1965, Ewel 1976, Swift et al. 1979, Edwards 1977) and site (Weigert and Murphy 1970, UNESCO 1978).

Species level differences were well documented. However, no one had looked at the decomposition rates of fresh leaf composites. Table 24 shows the species composition and the percentage of a species represented in each bag. Every bag was representative of the composition of the freshly fallen leaves in each plot at that time.

There were no significant differences in decomposition resulting from species composition or site nor were there significant differences in time of field placement up to 120 days. There appears to be a difference in decomposition due to the time of field placement after 120 days. This study is still in progress and seasonal-rainfall differences are yet to be verified. We conclude that neither species nor site influenced decomposition when the total group of species representative of an area was placed in a decomposition bag. This study demonstrates ecosystem level functioning in the decomposition process as well as leaf fall.

Turnover time (TOT) defined as the time necessary for leaf fall to replace leaf storage was 0.56 years. If only decomposition were involved, leaves should decompose 100 percent in 0.56 years, but this study indicates that decomposition was 75 percent in 1 yr. Thus, factors other than decomposition must account for the rapid TOT; some organic matter may be incorporated into soil organic matter or lost to

Table 24 . Species composition and g fresh weight/species in decomposition bags.

3 - 3x		3a - 3ax		4 - 4x	
Species	g	Species	g	Species	g
Gt	1.8	Gt	1.8	Dm	2.7
De	1.3	Mb	1.7	Sl	1.0
Mb	0.7	De	1.4	Cep	0.7
Cep	0.8	Hor	0.7	Al	0.7
Dm	0.6	Pg	0.7	Ca	0.6
Sl	0.6	Dm	0.6	Ok	0.5
Pia	0.6	Cos	0.6	Mb	0.5
Hor	0.3	Sl	0.5	Ld	0.5
Pg	0.4	Cep	0.3	Bs	0.3
Ld	0.3	Mr	0.2	De	0.3
Bc	0.2	Ld	0.1	Ol	0.3
Cos	0.2	Mt	0.1	Sp	0.2
Sp	0.2	Sb	0.1	Mr	0.2
Cp	0.2			Bc	0.1
Misc.	1.8	Misc.	1.2	Misc.	1.4
Total	10.0	Total	10.0	Total	10.0

Table 25. Numbers of invertebrates collected over 10 days, 8 nights, 9-22 June 1981.

	Day	Night
ARTHROPODA		
Arachnida		
Acarina		
Oribatidae		1
Araneida		
unidentifiable to family	1	2
Pholcidae		
unidentifiable to family	1	
Modismus sexoculatus		2
Araneidae		
unidentifiable to species	1	1
Leucage regnyi	1	2
Clubionidae	1	5
Linyphiidae		
Diplocephalus gloriae	1	
Thomisidae		
Epicaudus mutchleri		1
Salticidae	3	1
Collembola		
Entomobryidae		
Lepidocyrtinus sp.?		1
Insecta		
Ephemeroptera		
Leptophlebiidae?	1	
Blattodea		
Blattidae		1
Blattellidae		4
Cariblatta hebardi		2
Orthoptera		
Gryllidae		
Orocharis vaginalis or *terebrans*		4
Cyrtoxipha gundlachi		3
undetermined Trigonidinae		1
Isoptera		
Kalotermitidae		
Glyptotermes pubescens (winged)	3	2
Termitidae		
Nasutitermes sp.	1	
Psocoptera		
Lepidopsocidae	12	7
Polypsocidae		2
Epipsocidae		2
Psocidae		3

Continued table 25

	Day	Night
Tysanoptera		
Phlaeothripidae	8	10
Thripidae	5	2
Hemiptera		
Dipsocoridae	1	
Miridae		
undetermined species	1	
Polymerus pallidus	1	
Lygaeidae		6
Cydnidae	1	
Homoptera		
Membracidae		
Nessorchinus esbeltus	1	
Cicadellidae		
unidentified species	1	
unidentified species (nymph)	1	
Sibovea coffeacola		1
Ponana insularis		3
Xestocephalus maculatus		2
Delphacidae		
Ugyops occidentalis		1
Derbidae		
unidentified species	1	
Dawnaria sordidulum		9
Dysimia maculata		1
Patara albida		1
Cixiidae (nymph)	1	
Kinnaridae		
Quilessa fasciata	2	
Achilidae		
Catonia cinerea		1
Catonia dorsovittata (nymphs)	3	5
Amblycratus striatus? (nymphs)	8	7
Quadrana punctata? (nymphs)		1
undetermined species (nymphs)	2	
Tropiduchidae		
Ladella stali	1	8
Issidae		
Thiona borinquensis	3	
Colpoptera maculifrons	6	
Colpoptera brunneus	9	5
Neocolpoptera monticolens	1	
Psyllidae	1	3
Coccoidea	1	1

Continued table 25

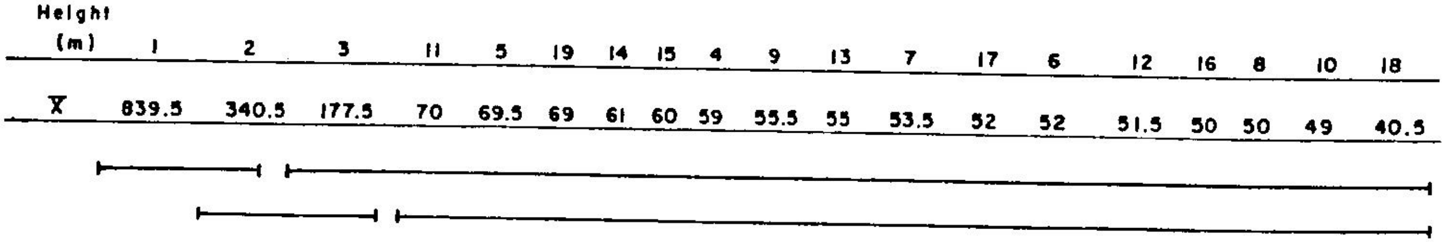
	Day	Night
Coleoptera		
Histeridae	4	1
Staphylinidae		
unidentified spp.	4	3
Palaminus sp.		1
Pselaphidae	3	
Ptiliidae		
Actinopteryx sp.	1	
Scaphidiidae		1
Elateridae		
Eucnemidae	4	2
Anobiidae		3
Trogositade (Tribe Tenebroidini)	1	
Cucujidae		2
Coccinellidae	3	3
Colydiidae		1
Tenebrionidae		1
Melandryiidae		1
Mordellidae	1	
Euglenidae	3	3
Chrysomelidae	1	2
Anthribidae	1	
Curculionidae		2
Scolytidae	7	7
Lepidoptera		
Cosmopterygidae?		1
Gelechiidae?		1
Gracialaridae?		1
Diptera		
Tipulidae	5	9
Psychodidae	9	11
Ceratopogonidae	102	80
Chironomidae	125	44
Mycetophilidae	18	4
Sciaridae	35	20
Scatopsidae	7	1
Cecidomyiidae	8	11
Asilidae		1
Empididae	14	4
Dolichopodidae	28	12
Phoridae	1520	1879
Pipunculidae	1	
Tephritidae	1	
Lauxaniidae	2	
Chamaemyiidae?	1	

Continued table 25

	Day	Night
Lonchaeidae	1	
Heliomyzidae	3	2
Chloropidae	3	
Agromyzidae	1	
Odiniidae	4	
Ephydridae	1	
Drosophilidae	3	3
Anthomyiidae	7	
Tachinidae	39	5
Calliphoridae	4	1
Sarcophagidae	1	
Hymenoptera		
Brachonidae	2	5
Ichneumonidae		1
Mymaridae	11	1
Trichogrammatidae	1	4
Eulophidae	6	2
Encyrtidae	54	18
Eupelmidae	8	
Agaonidae	2	
Torymidae	1	1
Pteromalidae		1
Cynipidae	1	
Ceraphronidae	3	
Diapriidae	4	
Scelionidae	29	14
Platygastridae	5	
Bethylidae	4	
Drynidae	1	1
Formicidae		
Monomorium floricola	1	
Iridomyrmex melleus	3	1
Myrmelachista ramulorum	1	4
Brachymyrmed heeri		1
unidentified workers	7	3
winged males	6	5
Sphecidae (Cabroninae)	4	

Table 26. Numbers of invertebrates collected (by order), for day, night, combined totals; and percentage composition of overall total. Day-night totals are from 10 days and 8 night samples.

Order	Day	Night	Total	%Overall Total
Acarina	0	1	1	.02
Araneidae	9	14	23	.51
Collembola	0	1	1	.02
Ephemeroptera	1	0	1	.02
Blattodea	0	7	7	.16
Orthoptera	0	8	8	.18
Isoptera	4	2	6	.13
Psocoptera	12	14	26	.58
Thysanoptera	13	12	25	.55
Hemiptera	4	6	10	.22
Homoptera	42	49	91	2.02
Coleoptera	33	28	61	1.35
Lepidoptera	0	3	3	.07
Diptera	1943	2087	4030	89.42
Hymenoptera	152	62	214	4.75
Totals	2213	2294	4507	100%



Height (m)	1	2	3	11	5	19	14	15	4	9	13	7	17	6	12	16	8	10	18
X̄	839.5	340.5	177.5	70	69.5	69	61	60	59	55.5	55	53.5	52	52	51.5	50	50	49	40.5

Figure 10. SS-STP for differences of mean numbers of insects among 1 m height intervals.

the system as export. Future studies should be directed toward investigating the fate of this unaccounted organic matter. It is essential to determine input, cycling, and export from a natural system in order to monitor effects of future perturbations.

5.4 Faunal Studies

5.4.1 Invertebrates

Subtask 1. Vertical Transect Sampling

A total of 4506 invertebrates representing 15 orders and 105 families (Table 25) were collected over the 10 day-8 night sampling period. Flies constituted the most abundant insect group (4030 or 89%) followed by Hymenoptera (214 or 5%), Homoptera (91 or 2%) and Coleoptera (61 or 1%) (Table 26). Phorid flies (representing several species) made up 75% of the entire invertebrate fauna and were obviously the dominant invertebrate group during the two week period. The Diptera comprised the most families (27) followed by Coleoptera (20) and Hymenoptera (19).

No significant difference in mean abundance of invertebrates was found between day and night samples, but there were significant differences among the mean number of invertebrates collected at the 19 heights ($F_{[.01]}(18,19) = 6.68$, $p < .001$). An SS-STP test (Figure 10) showed the first 2 m to contain a significantly greater number of invertebrates than the upper 17 m. The Phoridae likewise showed significant differences in mean numbers collected among the 19 m ($F_{[.01]}(18,19) = 6.68$, $P < .001$) and were the major contributing factor to the differences observed among total invertebrate groups. An SS-STP of Phorids showed the same results as for all invertebrates. When all invertebrates minus the Phoridae were compared, no mean differences were detected.

Members of the superfamily Fulgoroidea (Delphacidae to Issidae, inclusive, Table 25) or planthoppers are conspicuous herbivores in the rain forest. Though they are often seen and collected in sweep net and D-vac samples near the ground, more of these insects were found near the canopy than below. When the 19 m strata were divided into three equal samples of 6 m (the first meter sample was deleted because it had so few specimens) a significant difference occurred between the top 6 m and the lower 12 m (Figure 11).

Next to the Phorids the acalypterate families (Tipulidae to Cecidomyiidae, inclusive) were the most common group of insects and their numbers were relatively constant throughout the 19 m.

Discussion

The Diptera, and in particular phorid flies, were the most abundant flying insects at the tower. Phorids are a large group with varied habits. Adults and larvae probably feed on decaying organic matter and this explains their greater numbers near the ground. Phorids collected at 1 m above ground during separate 24 hour periods ranged from 0 to 913. No specimens were taken on 9 June, one was taken on 10 June, two on 11 June, six on 12 June, and 285 on 15 June, the next 24 hour sampling period. A culmination was reached on 16 June (913) but numbers were reduced to 84 on 17 June. The data indicate a sudden mass emergence over a short period of time. It is not known if several broods occur throughout the year, or whether these emergences are restricted to the wet season.

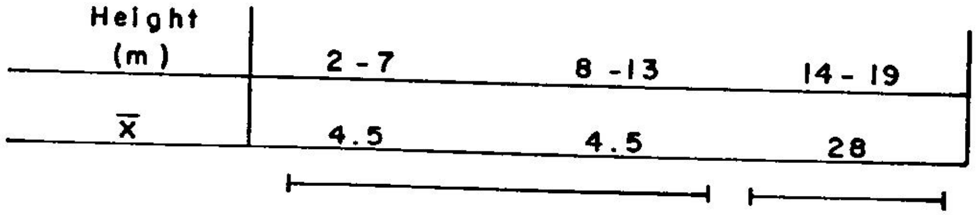
The small, inconspicuous nematoceran Diptera appear to be the most abundant insects on a regular basis. As weak flyers, they were probably caught passively by the sticky traps. Large invertebrates such as dragonflies and butterflies were generally absent from our samples and they may have avoided the traps or escaped by sheer strength when caught. The absence of Odonata, large Coleoptera and large Lepidoptera, all seen in the forest, support this belief.

Although no significant differences of mean numbers of invertebrates were detected between day and night, some groups showed a strong nocturnal preference (Blattodea - 7 night, 0 day; Orthoptera- 8 night, 0 day; Lepidoptera- 3 night, 0 day) while the dipteran suborders Brachycera and Cyclorrapha (except Phoridae) were strongly diurnal (114 day, 28 night).

Numbers for some orders were too low to establish meaningful results in stratification. Ideally, stratification studies of families of a single order would be useful for an overall picture of forest zones, but the Phoridae was the only family with sufficient numbers to show a significant difference. Significant stratification results

Figure 11.

SS-STP for differences of mean numbers of Fulgoroids per 6 meter increments (1st meter deleted)



Height (m)	2 - 7	8 - 13	14 - 19
$\overline{x}$	4.5	4.5	28

were observed for all invertebrates, but the difference was solely due to the presence of Phorids. The comparison of superfamilies, as with the Fulgoroidea, was useful in revealing vertical stratification within an order. The homopterans feed on phloem from leaves and small twigs which explains their abundance in the canopy, since the high canopy contains most of the leaves and small stems. Pscoptera are a relatively rare group, yet we collected 26 individuals from four families. Though Coleoptera comprise only 1.35% of invertebrates collected, they represented, next to the Diptera, the most families collected. This is probably due to their overwhelming taxonomic diversity as compared to other invertebrates. Most Hymenoptera collected were small to minute parasistic taxa from superfamilies Chalcidoidea and Proctotrupoidea which are primarily insect egg parasites. Among the hymenopterans collected were two male dryinids, rare wasps which are parasitic on homopterans, and two female agaonids, or fig wasps. Agaonids are obligate pollinators of fig trees and indicate the presence of fig trees in the forest.

One commonly accepted theory of the tropical rain forests is that a great diversity of forms exists at the expense of abundance of any one or few species. However, in this study, 75.30% of all invertebrates sampled consisted of members of one insect family, the Phoridae. This indicates that, like some temporate zone areas, some invertebrate groups may become very abundant and can comprise a significant component of the invertebrate biomass. The results are in agreement with Penny and Arias (1981), who after a year of light and trap sampling in the Amazon rain forest found 84 to 91% of the invertebrates to be Diptera, primarily Luzomyia spp. (Psychodidae).

Subtask 2. Macrodecomposers Associated With Leaf Litter Decomposition

A total of 2565 invertebrates were collected from 97 bags (Table 27) over a 120 day period. The seven day samples contained the lowest total sample size (442) and the 14 day samples the highest (602), a difference of 160 animals. Twenty eight day total samples (535) were similar to 120 day samples (519) and the 60 day total sample size (467) would have been higher had the total sample size have been 20 instead of 17. As expected, mites (Acarina) were the most abundant animals (1217 or 47.4%) followed by Diptera (503 or 19.6%) of which

Table 27. Macroinvertebrates associated with each collection of decomposition bags. Days indicate time of collection. Each column represents a collection from five 10 ounce (fresh weight) samples. Under 60 days, sample sizes for 4 and 4x are 4 and 3 bags respectively.

	7 days				14 days				28 days				60 days				120 days			
	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x
ARTHROPODA																				
Arachnida																				
Acarina																				
Oribatidae (sp.#1)	15			2	5	4	5	1	6		4	1		2					8	
Family? (sp.#2)	11	25	8	16	18	4	15	9		25			12	59	18	11	9	21	8	36
other species	39	24	9	10	30	19	21	65	78	43	55	120	29	117	19	3	12	44	56	66
Araneida																				
Dipluridae																				
Accola spinosa	1												1							
unidentifiable to family														1	1					
Pholcidae?	1		1		1															
Clubionidae?		1																		
Salticidae														1						
Phalangida																				
Gonyleptidae?																				1
Pseudoscorpionida																				
Ideoroncidae			1			1	1	3	1			2		1	1	1		3		1
Menthidae																				
Menthus sp.	1	1	2	2			3	8	3	6	3	10	3	9	5	1	1	1	2	4
Crustacea																				
Isopoda																				
Oniscidae																				
Philocia richmondi	1				2	3	1	2			2	7	4	4	13	14	5	51	8	13
Synurops granulatus																				
Subclass Copepoda?	5	3	4	11	25	17	1	14				1		8				1		8
Podocopa							5						4	1	2				8	6
Chilopoda																				
Geophilomorpha																				
Oryidae																				
Orphnaeus brevilabiatus							1								1					

Continued Table 27.

	7 days				14 days				28 days				60 days				120 days			
	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x
Scolopendromorpha																				
Cryptopidae																				
Scolopocryptus ferrugineus																		1		1
Diplopoda																				
Chordeumida																				
Stemmiulidae																				
Prostemmiulus heatwolus	1			1	4			10	1		2	2	1	1	11		1			1
Polydesmida																				
Cryptodesmidae																				
Docodesmus maldonadai										1	1				1			4	3	2
Glomeridesmida																				
Glomeridesmidae																				
Glomeridesmus marmoreus																		2	1	2
Polyzoniida																				
Siphonophoridae																				
Siphonophora portoricensis																	1			
Polyxenida?														1		1		1		
Collembola																				
Sminthuridae																				
Ptenothrix sp.					1	1	2						3	3						1
Sminthuroides sp.			2																	
Sphyrotheca sp.		1	2					12												
Entomobryidae																				
Dicranocentropha sp.	2	7	1	1		3	4	6					1	1		1	1			
Dicranocentruga sp.			3	1		2	3	6					2	8	1			2		3
Drepanocyrtus sp.?					2			1									1			
Lepidocyrtus sp.		1		1		5		1						2				1		
Lepidocyrtinus sp.								3												
Salina sp.									2											
Isotomidae																				
Proisotoma sp.					1				5										1	2
undetermined genus	1					1	2											1		
Poduridae		2	6	2		4		2							2		1	1		
Insecta																				
Blattodea																				
Blattellidae (nymphs)	2		1		7			1	4	1	1	1			1					

Continued Table 27.

	7 days				14 days				28 days				60 days				120 days			
	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x
Psocoptera																				
Liposcelidae			1	1					4					1				1	1	1
Psyllipsocidae																				
(brachypterous)	1			1				1				1	3	1	2			1		
Thysanoptera																				
Phlaeothripidae			1					6		2				1						
Hemiptera																				
Aradidae (nymph)															1					
Dipsocoridae (nymphs)		1				1									1*					
Schizopteridae																		1		
Homoptera																				
Cicadellidae																				
Deltocephalus flavicosta													1							
Empoasca sp.													1							
Graminella cognita														1						
Idiocerus myrciae?																			1	
Xestocephalus maculatus														1						
Cixiidae																				
Bothriocera undata																		1		
Pintalia alta													1							
Fulgoroidea (nymph)					1															
Coccoidea													4	2					3	
Coleoptera																				
Staphylinidae	1	2	2	3	3	1		1				1								
Pselaphidae																	1	3	1	
Ptiliidae																				
Actinopteryx sp.	2			1	2	9	4	1			1									
unidentified genus						1		1												
larvae +	3				1	9	2	3												
Ptilodactylidae																		2		
Lycidae? (larvae)					2															
Scolytidae	2	1	1			1	1	1				1	1	1	1			4	7	6

Continued Table 27.

	7 days				14 days				28 days				60 days				120 days			
	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x
Lepidoptera																				
Microlepidoptera (unidentified larvae)	1											1						1*		
Gracillaridae?														1						
Cosmopterygidae?																	1	1		
Gelechiidae?																1				
Gelechiidae or Oecophoridae (larvae)			1			1		3						3						
Tineidae									1										2	
Pyralidae (larva)	1																			
Arctiidae																				
larvae											1									
Talaria sp. (adult)														1						
Noctuidae (larvae)	4		1		1		2							1						
Diptera																				
Tipulidae (larvae)									2						1			1		
Psychodidae																				
larvae	1	1					1	1												
adults		1					2	1		1		1	4	7	1	1		2	2	2
Culicidae												1							1	
Ceratopogonidae																				
larvae			1		1	1	11	10				1		1						
adults	1			1			1	2	1	1	1	1	2	1						
Chironomidae																				
larvae and pupae	84	6	16	29	9	11	45	43			4	11							6	2
adults		7			1	2	6	1	2				4	1	1	1		2	12	2
Mycetophilidae										1			2					2		
Sciaridae	1												1	1			1	2		1
Scatopsidae										1										
Cecidomyiidae	2		1	1		1	1	1	3	2		2	1	2		1			3	
Stratiomyidae (larvae)	2		1	1	2		2				4	6								
Empididae									1											

Continued Table 27.

	7 days				14 days				28 days				60 days				120 days			
	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x	3a	3xa	4	4x
Dolichopodidae											1					1		1	1	
Phoridae			2		1		1	1	1	1		2		1				3	2	
Syrphidae																		1		
Piophilidae?									1							1				
Curtonotidae												1								
Drosophilidae																				
larvae	4	2	2		1		1	2												1
adults				1	1				5	4		2		1		1				1
Chloropidae							1													
Anthomyiidae? (larvae)				1		1		3	1	1		1		1				1		
Hymenoptera																				
Mymaridae																			1	
Cynipidae																			1	
Scelionidae								1												
Formicidae																				
<u>Odontomachus brunneus</u> (winged ♂)														1						
<u>Anochetus mayri</u>																	1			
<u>Strumigenys eggersi</u>					1															
<u>Tapinoma melanocephalum</u>															1					
<u>Camponotus ustus</u>																			1	
<u>Wasmannia auropunctata</u>													4							
<u>Pheidole moerens</u>	1										1									
<u>Monomorum floricola</u>‡																1		1		
<u>Solenopsis azteca</u>		1														1				
<u>Solenopsis corticalis</u>									45		1									
<u>Solenopsis</u> sp.	2	1			2															1
<u>Brachymyrmex heeri</u>																				
ant larvae and pupae									10	1	1							1		
Mollusca																				
shell-less species				2			1				1									
shelled species															1					
Annelida?																			1	

- ● adult
- \+ some specimens may be larval Staphylinids
- ‡ probably entered sample through Berlese Funnel in Lab.

nematoceran and brachyceran larvae (Tipulidae to Stratiomyidae, Table 27) made up 11.7% of the total. There appear to be no real differences among any of the plots: common arthropods (e.g. Menthus sp., staphylinid beetles, Actinopteryx sp.) found in one leaf litter sample of five bags were generally found in the other three samples of 15 bags. Other organisms (e.g. all Hemiptera, Homoptera) were rare and sporadically distributed in the bags through time. These results agree with data previously presented (section 5.3.3) which indicate that litterfall rates and other vegetative aspects of the forest are relatively homogeneous.

Though there appeared to be little difference in the invertebrate fauna among samples at any given collection period, there were changes of certain invertebrate groups through time. Larvae and pupae of midges (Chironomidae) were found in all four samples during the seven and 14 day periods but were scarce or absent thereafter. The following groups had distribution patterns similar to chrironomids, though because they were not as abundant, it is difficult to see as obvious a trend: Copopoda, Dicranocentropha springtails, blattellid nymphs, and drosophilid larvae. All of these organisms are probably important macrodecomposers. Both adults and larvae of feather winged beetles (Actinopteryx adults and larvae) were common only during the 14 day collection. Terrestrial isopods (Philocia richmondi) and to a lesser extent, cladocerans (Podocopa) were common only during the 60 and 120 day collections. Apparently, these two invertebrate groups prefer litter which has already reached an advanced state of decomposition.

Discussion

The results show that mites, the isopod Philocia richmondi, the millipede Prostemmiulus sp., entomobryid springtails and chironomid larvae were the most common invertebrates found in leaf litter bags and these organisms are probably the most important macrodecomposers. Menthid pseudoscorpions and staphylinid beetles were frequent in many samples but they are carnivorous arthropods. Their predatory activities (including defecation of prey remains) are probably important in aiding small microscopic organisms in decomposing leaf litter. Few ants were collected in the samples not because they were rare, but probably because these ambulatory insects escaped capture when litter bags were collected. Thus their importance in aiding the decomposition process of leaf litter is probably underestimated.

Mites were the most abundant arthropods in the leaf litter but they are small so their quantitative contribution to decomposition may not be as great as the larger isopods or chironomid larvae.

No obvious differences in arthropod species or numbers were observed for same day litter collections among plots. The commonly collected arthropods are probably widespread throughout the study area.

The most dramatic successional differences in arthropod species was between chironomid larvae and the terrestrial isopod _Philocia richmondi_. Chironomid larvae were common in all samples of 7 and 14 days but, except for 4 and 4x during 28 and 120 days, were absent in all later samples. _Philocia richmondi_ seems to prefer partially decomposed leaf litter. Only one specimen was found in any of the 7 day bags; low numbers were found in each 14 day sample and their numbers increased after 14 days. These two arthropod groups are probably important macrodecomposers as both are known to be detritus feeders.

McMahan and Sullins (1970) reported Hymenoptera (ants) to be the most abundant arthropods in their sampling of forest litter for El Verde, but their collection method (suction apparatus) was more likely to collect ants. They did not count larval insects in their studies but our results indicate that holometabolous insect larvae are probably a significant component of the leaf litter ecosystem.

Subtask 3. _Anolis_ Food Habits

One hundred thirty eight stomachs were examined (Table 2) which had a total of 1989 items comprising at least 169 different taxa (Table 28). No _Anolis_ were found with empty stomachs, but several did have only one item. Some had eaten their own skin and these were the only contents in some specimens. The greatest quantity in numbers and species of prey was taken by an _A. evermanni_ female from the Rio Sonadora (hereafter called "creek"). It had 77 items representing 21 species (20 species of invertebrates, one species of seed). Although mites appear to the most abundant arthropods in the forest, ants, primarily _Myrmelachista ramulorum_, _Iridomyrmex melleus_ and _Pheidole_

Table 28. Prey taxa consumed by four species of *Anolis* in dry and wet seasons.

Taxon	*A. gundlachi*				*A. evermanni*						*A. stratulus*				*A. cuvieri*
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
ARTHROPODA															
Pseudoscorpionida															
Menthidae	1					1	1								
Phalangida															
Gonyleptidae		1	1	1											
Acarina															
Oribatidae			1					2		1	2	5	1	1	
Other families		2								1					
Araneida (unidentifiable to family)		3	1		1	2	2	7		4	2	2			
Theraphosidae															
Cyrtophilos portoricae (young)					1										
Uloboridae															
Miagrommopes ciliatus							1								
Pholcidae															
Micromerys dalei		1								1					
Other species				2	1	1				1	1				
Araneidae															
Gasteracantha tetracantha							2								1
Leucage regnyi						3		1	1	1					
Capichometa jayuyensis								1							
Other species			1	2				1	1	1					
Clubionidae				1					1						
Sparassidae					1	1									
Salticidae	1	1		1		1		1	2	1				1	
Lyssomanidae															
Lyssomanes portoricensis								1							

Taxon	A. gundlachi				A. evermanni						A. stratulus				A. cuvieri
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Isopoda															
Oniscidae	1														
Diplopoda															
Glomeridesmidae															
Glomeridesmus marmoreus	1														
Polydesmidae															
Docodesmus maldonadai		1													
Stemmiulidae															
Prostemmiulus sp.				1											
Chilopoda															
Henicopidae															
Lamyctes nesiotes										1					
Collembola															
Sminthuridae															
Spyrotheca sp.		1													
Entomobryidae															
Lepidocertinus sp.						1									
Isotomidae								1							
Poduridae				1								1			
Archaeognatha															
Machilidae						1		1							
Ephemeroptera															
Leptophlebiidae?				3				1	2	3					
Odonata															
Coenagrionidae															
Telebasis vulnerata									1						
Blattodea (unidentifiable to family)	1				1										
Blattidae		1	1												
Blattellidae		1						1*	1	2		1			
Plectoptera sp.				1		1	1			1				1	
Cariblatta sp.								1							
Phasmodea															
Phasmatidae															
Clonistria sp.															1
Lamponius sp.						1									1

Taxon	*A. gundlachi*				*A. evermanni*						*A. stratulus*				*A. cuvieri*
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Orthoptera (unidentifiable to family)															1
Gryllidae				2				1	1	5					
Orocharis sp.						1									
Anaxipha sp.						1									
Cyrtoxipha sp.								1							
Gryllus assimilus	1			1											
Anurogryllus muticus	3	1													
Subfamily Nemobiinae										11					
Dermaptera		1					1					1			
Isoptera (unidentifiable to family)				1					1						
Kalotermitade															
Glyptotermes pubescens	1				1				2						
Termitidae															
Nasutitermes costalis									2						
Embioptera															
Terebratemidae											1				
Psocoptera (unidentifiable to family)												1			
Polypsocidae								3							
Epipsocidae								1	3	1					
Thysanoptera															
Phalaeothripidae				51		2									
Hemiptera															
Veliidae															
Rhagovelia sp.	3								4	7					
Microvelia sp.									1						

Taxon	A. gundlachi				A. evermanni						A. stratulus				A. cuvieri
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Saldidae															
Micrancantha sulcata			7			1				11					
Dipsocoridae											1				
Schizopteridae						1									
Phymatidae															
Phymata marginata														1	
Enicephalidae?														1	
Reduviidae															
Zelus subimpressus			1				1	1						1	
nymphs of undetermined species							1								
Homoptera															
Cicadellidae															
Sibovea coffeacola													1		
Xestocephalus maculatus	2			1	2	1	1	1	1						
Fulgoroidea				1	1		1	3			1	2			
Fulgoroidea nymphs	1				1	3	2	3						1	
Cixiidae				1											
Bothriocera undata								1	1				1		
Pintalia alta									1	1		1	1		
Delphacidae															
Ugyops occidentalis	1				1									1	
Achilidae						1						1			
Tropiduchidae															
Ladella stahli			1				3	2	1					2	
Parahydriena hyalina or n. sp.							2			1					
Flatidae															
Petrusa roquensis										1					
Petrusa torus				1				1						1	
Flatormes stylata						1									

Taxon	A. gundlachi				A. evermanni						A. stratulus				A. cuvieri
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Issidae															
Thiona boringuensis			1	1			1	1		1				4	
Colpoptera brunneus								1							
Neocolpoptera sp.							1	1	1					1	
Kinnaridae															
Quilessa sp.							1								
Psyllidae		1			1		5	2						3	
Aphididae	1														
Coccoidea						1		5					1	5	
Neuroptera															
Chrysopidae										1					
Coleoptera															
(unidentifiable to family)		1		1			1		2	1		2		3	
Staphylinidae	1														
Scarabaeidae		1			1										
Dryopidae										4					
Lampyridae				1	2				2						
Melyridae?				1											
Cucujidae	1	1													
Nitidulidae		2													
Coccinellidae				1			4								
Colydiidae (larva)						1									
Euglenidae						2									
Chrysomelidae				3			1		2	5				1	
Cerambycidae															1
Curculionidae.		2					1	1		2	1				

Taxon	A. gundlachi				A. evermanni						A. stratulus				A. cuvieri
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Diaprepes abbreviata															1
Scolytidae	1	18	4	5		2				2	2	2		1	
Coleoptera larvae		5			2		1	1	2	1					
Trichoptera (undeterminable to family)							1	1							
Philoptomatidae															
Chimarra maldoni					1										
Psychmyiidae															
Xiphocentron boringuensis									1	1					
Hydroptilidae															
Alisotrichia hirudopsis			24												
Lepidoptera															
Hesperiidae (larva)			1												
Sphingidae (larvae)															2
Pericopidae or Arctiidae (larvae)							1	2							
Noctuidae (adults and larvae)		16				1				1	2				
Geometridae (larvae)								1						1	
Pyralidae (adults and larvae)				3		1									
Tortricidae or Gelechiidae			1	2	2	4	2	2		9				5	
Psychidae?							1								
Acrolophidae (adults and larvae)			2							1					
other microlepidoptera	2	3		9		6	4		2	1		1	2		
Diptera															
Tipulidae			1			1	2		14	5					
Psychodidae			1			1	3	1		9	2		2	1	
Ceratopogonidae						1	1		2	2	1		2		

Taxon	<u>A. gundlachi</u>				<u>A. evermanni</u>						<u>A. stratulus</u>				<u>A. cuvieri</u>
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
Chironomidae (larvae)		58	1			1		1	1	5		1			
Chironomidae (adults)			1						1	1					
Sciaridae					1	2	6	8		1		5	2		
Cecidomyiidae								2	1	1					
non identifiable Nematocera		2		1	1			1				4		2	
Stratiomyidae (larvae)			5							10					
Empididae				2		2				10					
Dolichopodidae				2						4					
Phoridae		1													1
Syrphidae? (larva)	1														
Lauxaniidae?													1		
Ephydridae										2					
Chloropidae										1					
other Acalypteryate families				1			1	1						1	
Acalypterate larvae		3						1		1					
Hymenoptera															
Brachonidae	1											1	1		
Ichneumonidae				1											
Chalcidoidea				2			1			5	1	5		2	
Diapriidae									1	5					
Scelionidae							1		1			1			
Vespidae															
<u>Mischocyttarus</u> <u>cubensis</u>	1														
Apidae															
<u>Apis</u> <u>mellifera</u>	1				1			1	1						
Formicidae															
<u>Odontomachus</u> <u>brunneus</u>		2		1			1		1				1		1

Taxon	*A. gundlachi* dry ♂	*A. gundlachi* dry ♀	*A. gundlachi* wet ♂	*A. gundlachi* wet ♀	*A. evermanni* dry ♂	*A. evermanni* dry ♀	*A. evermanni* wet ♂	*A. evermanni* wet ♀	*A. evermanni* creek ♂	*A. evermanni* creek ♀	*A. stratulus* dry ♂	*A. stratulus* dry ♀	*A. stratulus* wet ♂	*A. stratulus* wet ♀	*A. cooperi* wet ♂ & ♀
Anochetus mayri		2							1						
Strumigenys rogeri			2	1					3						
Cyphomyrmex rimosus			1	1											
Tapinoma littorale		1										3			
Camponotus ustus						2				1		1	5		
Trachymesopus stigma	1		1												
Hypoponera ergatandria									1						
Myrmelachista ramulorum		1	1		53	23	2	5	8	7	25	33	29	12	
Brachymyrmex heeri		3		4	2		1	15	7	4		1	1	3	
Iridomyrmex melleus	4	4	5	1	41	12	63	28	45	2	8	3	3	19	
Paratrachina sp.		1	2			1				1					
Mycocepurus smithi		1		5					1						
Wasmannia auropunctata				2					23	12			1	1	
Tetramorium guineense									1						
Pheidole subarmata				6											
Pheidole moerens	3	35	8	18		5		4	1	22		1	1		
Pheidole sp.			1												
Monomorium floricola										10					
Solenopsis azteca												1		2	
Solenopsis corticalis									3						
Solenopsis sp.		18		2		1		23	5		1	4		3	
other species	4								1	3	1	5	1	2	
winged ♂♂ Formicidae		1	3	5		2	2	1	41	4			1	1	
larvae and pupae					41	7								7	
NEMATODA?				1	1		1								
ANNELIDA															
Oligochaeta	1		3	1											
MOLLUSCA															
Class Gastropoda	1						1								4

Taxon	*A. gundlachi*				*A. evermanni*						*A. stratulus*				*A. cuvieri*
	dry		wet		dry		wet		creek		dry		wet		wet
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂ & ♀
CHORDATA															
Anura															
Eleutherodactylus coqui		1	1?												
Squamata															
Anolis gundlachi (tail) piece)															1
Anolis skin			1												
Lichens debris		1		1		1	1	2		1				2	2
Leaf debris						1	2			2	1	2			
Misc. seeds					1				1	1				1	1
Cecropia peltata (seeds)					6				32		1	1			
Casearia arborea (seeds)									71						
Stones									3						

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*egg case

moerens were the most numerous prey items. A wide variety of organisms were taken by all four species although some (Acarina, Collembola, leaf debris, lichen-moss debris, and rocks) were probably ingested accidentally or inadvertently while securing another prey item. Anolis cuvieri seemed to confine themselves primarily to medium sized gastropods and large phasmatids. One female A. cuvieri attempted to seize a full grown male A. gundlachi but succeeded only in getting a part of the tail.

Average size prey for each Anolis group is shown in Table 29 and Figure 12. Anolis cuvieri, as expected, had the largest average prey size (22.2 mm) but the fewest mean number of taxa (1.7). Because of sexual dimorphism, large male wet and dry season A. gundlachi had larger mean prey sizes (6.6 and 6.4 mm respectively) compared to females of both seasons (2.6 and 2.7 mm). The longest prey item was an earthworm (about 130 mm) taken by a male wet season A. gundlachi. Mean prey sizes for all other lizards are similar and range from 2.4 to 3.0 mm. Few lizards were totally carnivorous and the mean percent animal volume for creek A. evermanni males was only 59% (Table 30) and indicates that this species (and probably others) will eat considerable amounts of vegetable matter from time to time.

Because minute differences in prey dimensions are accentuated when volumes are calculated, greater differences were observed among lizards when this parameter is measured (Table 30). Anolis cuvieri had the greatest mean volume (1223.6 mm^3) followed by wet season male A. gundlachi (1093.9 mm^3). Except for the wet season females, all A. gundlachi had greater mean volume estimates than did A. evermanni. If only mean animal volumes are compared, then all A. gundlachi estimates surpass estimates of A. evermanni. Wet season A. stratulus had almost double mean volume estimates over dry season species despite similar mean prey size estimates (Figure 12) and shows that these lizards may be food limited during the dry season.

There was little difference between mean volume estimates of wet and dry season A. evermanni but there were large differences between males and females. The results may be due to sampling error or to different predatory habits between sexes between wet and dry seasons. Except for male wet season A. evermanni, creek A. evermanni had greater mean food volumes than all of the forest A. evermanni. Except

Table 29. Stomach contents for four species of _Anolis_ lizards during dry and wet seasons. N=number of lizards per group.

		mean no. taxa/ lizard	mean no. animal taxa/ lizard	mean no. animals/ lizard	mean size animal prey/ lizard group (mm)	mean % no. animals/ lizard
A. cuvieri	♂ & ♀ wet (N=10)	1.7	1.5	1.6	22.2*	89**
A. gundlachi	♂ dry (N=10)	3.5	3.5	3.9	6.6	100
	♀ dry (N=10)	7.0	6.9	20.2	2.6	98
	♂ wet (N=8)+	4.8	4.8	10.5	6.4	100
	♀ wet (N=10)	7.7	7.5	16.2	2.7	98
A. evermanni	♂ dry (N=9)	4.1	4.1	16.8	2.3	93
	♀ dry (N=8)	7.8	7.6	13.3	3.0	98
	♂ wet (N=9)	7.1	7.0	15.1	3.0	98
	♀ wet (N=10)	8.8	8.7	15.4	2.7	97
	♂ creek wet (N=10)	7.6	7.0	20.6	2.6	77
	♀ creek wet (N=10)	11.4	10.9	22.6	2.7	90
A. stratulus	♂ dry (N=8)	3.4	3.3	6.9	2.4	97
	♀ dry (N=10)	5.3	5.0	10.4	2.2	97
	♂ wet (N=4)	6.5	6.5	15.8	2.7	100
	♀ wet (N=9)	5.4	5.4	10.7	2.7	100

* N=8

** N=9

\+ sample size was 10 but one had _Anolis_ skin, another unidentified material (coqui muscle tissue?) and were not counted.

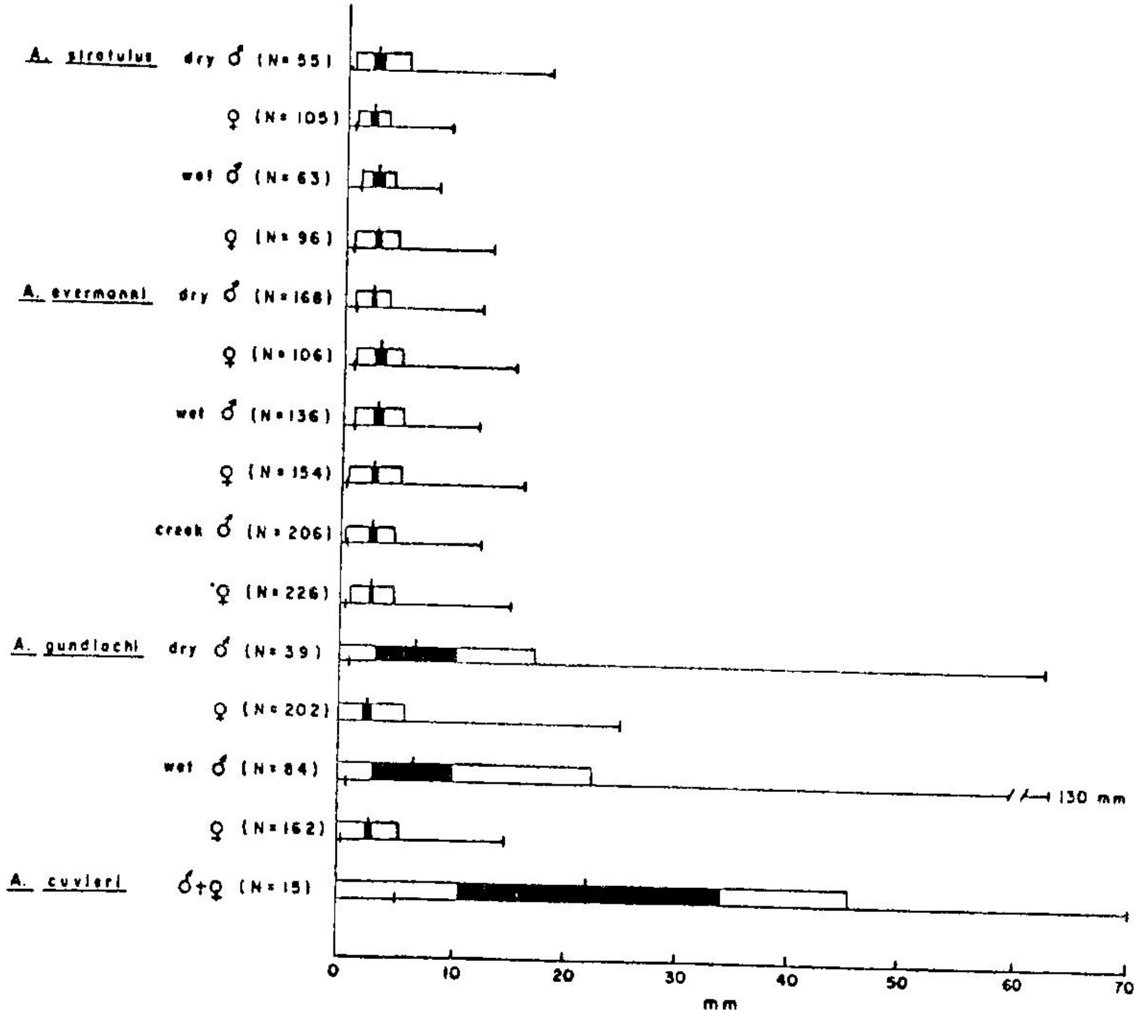

Figure 12. Mean prey size for Anolis at El Verde. For each variable, midpoint = mean, horizontal line = range, black portion of each bar = 1.96 standard errors on each side of mean, one half of each black bar plus white bar at either end = one standard deviation.

Table 30. Stomach contents for four species of *Anolis* lizards during dry and wet seasons. N=number of lizards per group. All volume estimates are mm^3.

			mean volume/ lizard	mean animal volume/lizard	mean % animal volume/lizard
A. cuvieri	♂ & ♀	wet (N=9)*	1223.6	1064.7	93
A. gundlachi	♂	dry (N=10)	583.1	583.1	100
	♀	dry (N=10)	514.3	514.0	~100
	♂	wet (N=9)+	1093.9	1093.9	100
	♀	wet (N=10)	242.5	242.4	~100
A. evermanni	♂	dry (N=9)	123.1	119.9	97
	♀	dry (N=8)	110.0	106.0	96
	♂	wet (N=9)	197.5	170.3	86
	♀	wet (N=10)	115.2	113.3	98
	♂	creek wet (N=10)	294.5	174.5	59
	♀	creek wet (N=10)	161.1	132.8	82
A. stratulus	♂	dry (N=8)	63.3	63.2	~100
	♀	dry (N=10)	50.6	48.8	97
	♂	wet (N=4)	97.8	97.8	100
	♀	wet (N=9)	104.4	84.4	81

* sample size was 10 but one sample (unidentified material) could not be measured.

\+ sample size was 10 but one had *Anolis* skin and could not be measured.

for wet season A. stratulus, male Anolis had greater mean volumes than their females of the same season, but females had greater numbers of taxa compared to males of the same season.

Most animals eaten were mature (Figure 13). Female lizards ate slightly higher percentages of larvae relative to males. No invertebrate larvae were found in stomachs of dry season A. stratulus.

We classified animal prey taxa into predators, herbivores, and scavengers. The last category included mites, millipedes, sow bugs, all fly larvae, most adult flies, and ants. Although ants were the most numerous prey items, their small mean volume size contributed less to the diet makeup than did herbivorous prey (Figure 14). Large planthoppers and orthopterans are bulky and primarily accounted for the great herbivore biomass consumed by all species. Snails and walkingsticks made up the major part of the herbivore biomass in A. cuvieri. Spiders were the largest contributor to the predatory biomass. Only five spiders were consumed by A. stratulus and accounted for low percentages of predator biomass in that species. Specimens of all Anolis species were found which had eaten their own skin.

Discussion

Identification of invertebrate taxa to lowest taxonomic levels did aid in the further understanding of prey availably for Anolis. Greatest differences were observed among ants because they were the most commonly consumed organisms. Three species of ants, Iridomyrmex melleus, Pheidole moerens, and Myrmelachista ramulorum are very common in the forest but they do not necessarily occur in the same habitats. Other scientists in the Luquillo forest have noted that M. ranulorum is primarily an arboreal species. We have found this species to be associated with birds; they are commonly used in feather maintenance (Waide, pers. comm.). The vertical transect studies indicated that M. ranulorum was found above 3 m (others were found at 1 m, 1 at 3 m, 1 at 11 m, 2 at 13 m). None were found in the litter samples (see subtask 2). Myrmelachista ranulorum was commonly found in several individuals of A. evermanni and A. stratulus but only two specimens were found in A. gundlachi. On the other hand, Pheidole moerens were

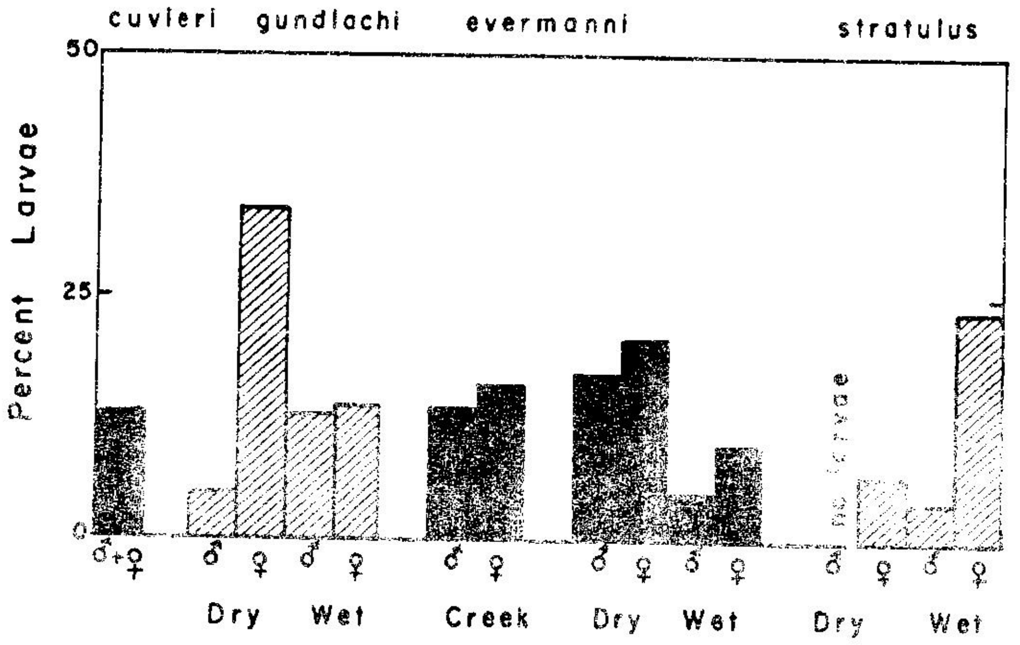

Figure 13. Percent invertebrate larvae consumed by *Anolis*.

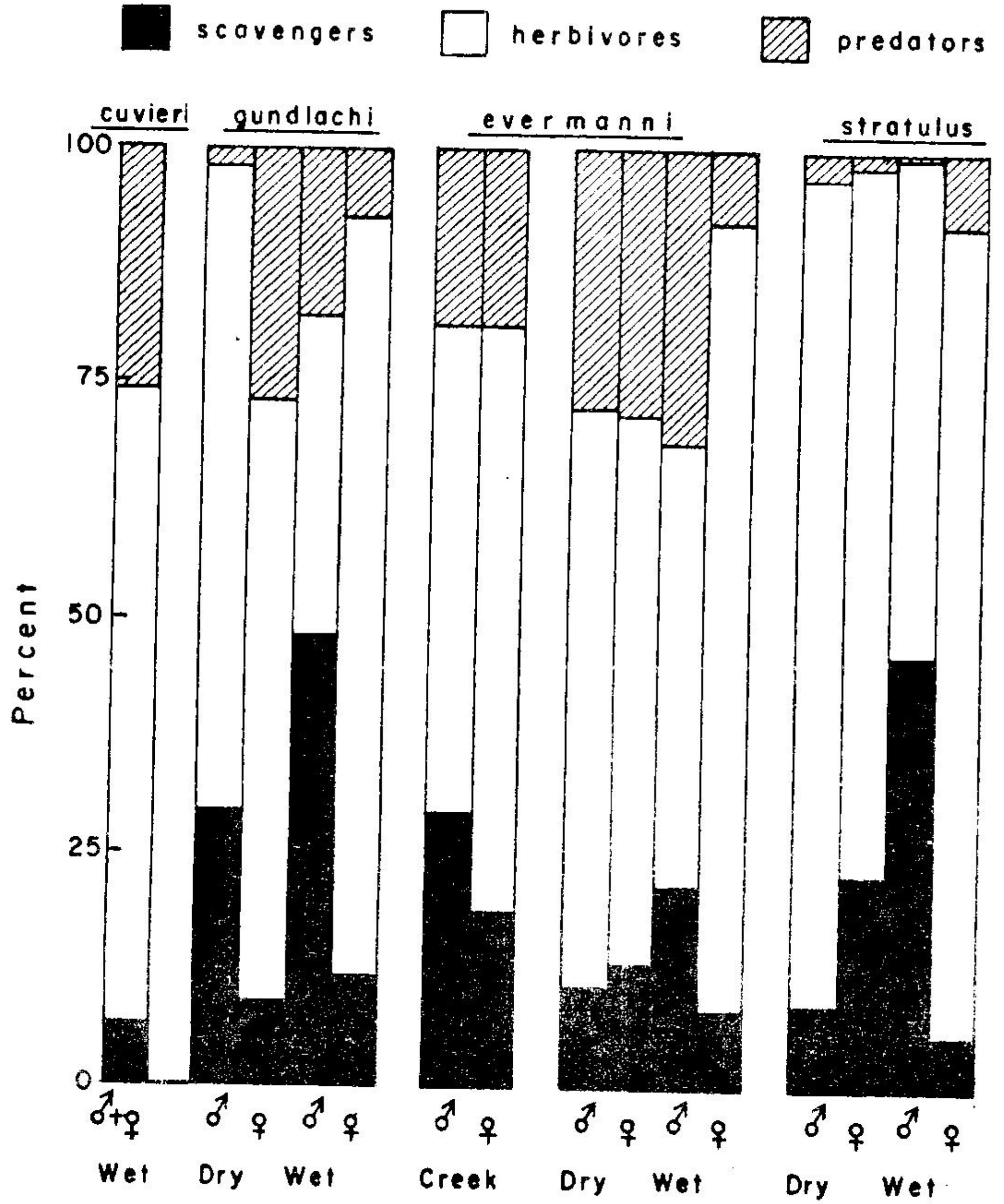

Figure 14. Percent invertebrate scavengers, herbivores, and predators consumed by Anolis.

found almost exclusively in A. gundlachi and in six female A. evermanni at the creek (a ground habitat). Only one P. moerens was found in a female dry season A. stratulus. Iridomyrmex melleus were commonly found in all three species of lizards. Two reasons can be postulated for the observed predation patterns: 1) the lizard species are ant specific, actively choosing one species over another, or 2) the diet "preference" is a result of the habitat selection of the lizards. We believe the second hypothesis is suitable because Anolis probably cannot discriminate between various species of ants. They probably attempt to eat any moving object within a given size range. Thus, Iridomyrmex probably occurs from ground level to the canopy and is therefore preyed upon by all Anolis species. Pheidole moerens is primarily a ground ant, and M. ranulorum a canopy species and each is primarily preyed upon by Anolis species which inhabit those stratified areas of the forest. Though numbers are few, the data indicate that Strumigenys rogeri and Mycoceperus smithi are primarily ground inhabiting species because they are consumed by A. gundlachi and creek A. evermanni.

Two large, primarily terrestrial inhabiting crickets, Gryllus assimilus and Anurogryllus muticus, were found only in A. gundlachi and creek A. evermanni (Table 28). Crickets of the genera Anaxipha and Cyrtoxipha are small, slender, arboreal (canopy) crickets and these insects were found only in A. evermanni and A. stratulus. Knowledge of the habitats of these crickets also correlates with the vertical distribution patterns of the three species of Anolis.

Veliids and saldids are water surface and shore inhabiting bugs respectively. They were found in stomachs of creek A. evermanni and are proof that these lizards feed near the stream. Interestingly, seven saldids and three veliids were also found in specimens of A. gundlachi which further implies a terrestrial habitat for this species.

The large, bulky, herbivorous planthoppers (Cixiidae to Fulgoroidea, Table 28) were most commonly found in arboreal A. evermanni and A. stratulus and parallel findings with the vertical transect sampling experiment (Subtask 1).

In summary, the following conclusions were derived from this study:

- The four species of Anolis are probably not prey specific. The apparent food specificity observed by various species of Anolis is due to coincidental vertical and horizontal (forest, stream) distribution patterns of lizards and prey.
- Male lizards generally eat greater amounts of food than their females of the same season, but females ingest greater numbers of prey resulting in a greater diversity of taxa.
- Anolis stratulus, the most abundant lizard in the forest appears to be the only species which is food limited during the dry season compared to wet season.
- Ants, planthoppers, lepidoptera larvae, and spiders appear to be the most important prey taxa.

5.4.2 Amphibians and Reptiles

Subtask 1. Species Inventory

All species known to inhabit the tabonuco forest near El Verde, are listed in Table 31. Information was compiled from existing literature (Turner and Gist 1970, Rivero 1978), specimens in the El Verde Field Station collection, and from surveys conducted during Phase I. No new species were observed in the study area during Phase I, and all species previously known to occur within the forest were found during the course of field studies with the single exception of Anolis occultus.

The presence and general abundance of common species appears to be unchanged since the intensive studies performed in the area during the 1960s. Differences in abundance estimates discussed in Subtask 4 are the results of different census techniques and probably do not reflect changes in actual abundances.

Subtask 2. Presence and Relative Abundance of Amphibians

Results of amphibian abundance surveys conducted during wet season 1980 are presented in Table 32. Eleutherodactylus coqui was by far the most abundant species observed in all four sampling locations. E. wightmanae, a smaller species, was second in abundance and was the only other species found in all areas. Although E. hedricki was heard calling within each of the four sample plots, its densities were suf-

Table 31. Vertebrates recorded from the El Verde Study Area.

Name	Status
Class: Amphibia[1]	
Order: Salientia	
Family: Bufonidae	
Giant Toad (*Bufo marinus*)	
Family: Leptodactylidae	
Coqui (*Eleutherodactylus coqui*)	abundant (40,000/ha)[2]
Mottled Coqui (*E. eneidae*)	
Tree-hole Coqui (*E. hedricki*)	
Forest Coqui (*E. portoricensis*)	
Ground Coqui (*E. richmondi*)	
Wrinkled Coqui (*E. wightmanae*)	
White-lipped Frog (*Leptodactylus albilabris*)	
Class: Reptilia[1]	
Order: Squamata	
Suborder: Lacertilia	
Family: Gekkonidae	
Upland Gecko (*Sphaerodactylus klauberi*)	
Common Dwarf Gecko (*S. macrolepis*)	
Family: Iguanidae	
Lagartijo Verde (*Anolis evermanni*	
Puerto Rican Giant Anole (*A. cuvieri*)	
Yellow-bearded Anole (*A. gundlachi*)	abundant (2,000/ha)[3]
Pigmy Anole (*A. occultus*)	rare
Lagartijo Manchado (*A. stratulus*)	abundant (25,000/ha)
Family: Anguidae	
Culebra de Cuatro Patas (*Diploglossus pleei*)	
Family: Amphisbaenidae	
Culebra Ciega (*Amphisbaena caeca*)	
Suborder: Serpentes	
Family: Boidae	
Puerto Rican Tree Boa (*Epicrates inornatus*)[4]	rare
Family: Colubridae	
Ground Snake (*Alsophis portoricensis*)	
Class: Aves[5]	
Order: Falconiformes	
Family: Accipitridae	
Red-tailed Hawk (*Buteo jamaicensis*)	
Broad-winged Hawk (*Buteo platypterus*)	
Sharp-shinned Hawk (*Accipiter striatus*)	rare
Order: Columbiformes	
Family: Columbidae	
Red-necked Pigeon (*Columba squamosa*)	abundant
Zenaida Dove (*Zenaida aurita*)	
Ruddy Quail-Dove (*Geotrygon montana*)	

Name	Status
Order: Psittaciformes	
Family: Psittacidae	
Puerto Rican Parrot (*Amazona vittata*)[4,6]	rare
Order: Cuculiformes	
Family: Cuculidae	
Puerto Rican Lizard Cuckoo (*Saurothera vieilloti*)	
Order: Strigiformes	
Family: Strigidae	
Puerto Rican Screech Owl (*Otus nudipes*)	
Order: Apodiformes	
Family: Trochilidae	
Puerto Rican Emerald (*Chlorostilbon maugaeus*)	
Green Mango (*Anthracothorax viridis*)	rare
Order: Coraciiformes	
Family: Todidae	
Puerto Rican Tody (*Todus mexicanus*)	abundant
Order: Piciformes	
Family: Picidae	
Puerto Rican Woodpecker (*Melanerpes portoricensis*)	
Order: Passeriformes	
Family: Tyrannidae	
Stolid Flycatcher (*Myiarchus stolidus*)	rare
Loggerhead Kingbird (*Tyrannus caudifasciatus*)[6]	rare
Family: Mimidae	
Pearly-eyed Thrasher (*Margarops fuscatus*)	
Family: Turdidae	
Red-legged Thrush (*Mimocichla plumbea*)	
Family: Vireonidae	
Puerto Rican Vireo (*Vireo latimeri*)	rare
Black-whiskered Vireo (*V. altiloquus*)[7]	abundant
Family: Parulidae	
Black and White Warbler (*Mniotilta varia*)[8]	
Parula Warbler (*Parula americana*)[8]	
Cape May Warbler (*Dendroica tigrina*)[6,8]	
Black-throated Blue Warbler (*D. caerulescens*)[8]	
Prairie Warbler (*D. discolor*)[8]	
Elfin Woods Warbler (*D. angelae*)[4]	rare
Ovenbird (*Seiurus aurocapillus*)[8]	
Louisiana Waterthrush (*Seiurus noveboracensis*)[8]	
American Redstart (*Setophaga ruticilla*)[6,8]	
Family: Coerebidae	
Bananaquit (*Coereba flaveola*)	abundant
Family: Thraupidae	
Blue-hooded Euphonia (*Euphonia musica*)	rare
Stripe-headed Tanager (*Spindalis zena*)	
Puerto Rican Tanager (*Nesospingus speculiferus*)	abundant
Family: Icteridae	
Black-cowled Oriole (*Icterus dominicensis*)	rare
Family: Fringillidae	
Puerto Rican Bullfinch (*Loxigilla portoricensis*)	

Name	Status
Class: Mammalia[1]	
Order: Chiroptera	
Family: Phyllostomatidae	
Greater Antillean Long-tongued Bat (*Monophyllus redmani*)	
Fruit Bat (*Artibeus jamaicensis*)	abundant
Red Fruit Bat (*Stenoderma rufum*)	
Brown Flower Bat (*Erophylla bombifrons*)	
Order: Rodentia	
Family: Muridae	
Roof Rat (*Rattus rattus*)	abundant
Order: Carnivora	
Family: Viverridae	
Small Indian Mongoose (*Herpestes auropunctatus*)	

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[1] Common and scientific names from Philibosian and Yntema (1977)

[2] Woolbright and Stewart (personal communication 1982)

[3] Turner and Gist (1970)

[4] Listed as endangered (U.S. and Puerto Rico)

[5] Common and scientific names from Bond (1971)

[6] Recher (1970)

[7] Summer resident

[8] Winter resident

Table 32. Anurans observed along transects during 1980 wet season surveys.[1]

	Average Number Observed[2] Plot No.				Relative Abundance Transect No.				
Species	1	2	3	4	1	2	3	4	Average Abundance
Bufo marinus	-	-	0.3	-	-	-	1%	-	1%
Leptodactylus albilabris	0.3	0.3	-	-	1%	1%	-	-	1%
Eleutherodactylus coquí	43.7	45.3	31.0	28.0	96%	93%	93%	93%	94%
E. wightamanae	0.3	2.0	1.7	0.7	1%	4%	5%	2%	3%
E. portoricensis	0.3	1.0	-	0.7	1%	2%	-	2%	1%
E. hedricki	-[3]	-[3]	0.3	0.7	-	-	1%	2%	1%
E. richmondi	1.0	0.3	-	-	2%	1%	-	-	1%

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[1] Surveys conducted September 26, 27, 28, 1980 and 25, 26, 29 October, 1980.

[2] Three replicates per transect.

[3] Heard calling in plot.

ficiently low that it was only recorded along two of the four transects.

Preliminary population density estimates were obtained by Larry Woolbright (SUNY Albany) who, using multiple mark and recapture surveys in the study area, calculated an estimate of 2,900 adults/ha and a total population density of coquis (adults, subadults, and juveniles) of 43,500/ha (Larry Wolbright, pers. comm.). The high density and generally uniform distribution of this species throughout the forest (at and near ground level) strongly indicate the importance of this species in the nocturnal food web.

Subtask 3. Anolis food Habits

Detailed analyses of gut contents were conducted on the four forest species (Anolis gundlachi, A. evermanni, A. cuvieri, and A. stratulus). The results of these analyses are presented in section 5.4.1, subtask 3.

Subtask 4. Anolis Population Densities

The initial program design provided for relative abundance studies based on minimum population density estimates (Overton 1971). Population density studies had not been planned because of the existing information provided by Turner and Gist (1970) on what was then thought to be the two most common species, Anolis gundlachi and A. evermanni. The discovery of large numbers of A. stratulus in the forest canopy (see subtask 5) part way into Phase I demanded absolute population density studies because of the potential importance of this species in terms of biomass and overall trophic structure. Data on relative abundance and density estimates for A. stratulus are presented below.

a. Minimum population densities of the three common anole species (Anolis gundlachi, A. evermanni, and A. stratulus) were obtained by Frye's strip census technique (Overton 1971). Because of known differences in approachability for different anole species (Heatwole 1968), separate mean distances were calculated for each species in the overall calculation of relative abundance. Results are presented in Table 33.

Anolis gundlachi was the most abundant and *A. evermanni* the second most abundant species in the study area during wet and dry seasons, based on ground level transects. Seasonal trends were consistent among plots. *A. evermanni* and *A. stratulus* increased in relative abundance during the dry season at the expense of *A. gundlachi*. Vertical studies (Subtask 5) suggest that these differences result in part from a shift in the vertical distribution of lizards from the canopy toward ground level rather than indicating a change in absolute population densities.

A. cuvieri was observed twice along transects and was infrequently encountered in the course of other Phase I field studies. Nine of the 10 individuals sighted were females and all were seen near ground level during the wet season suggesting that egg deposition may be the primary stimulus for coming to ground level. The species normally inhabits the forest canopy (Rand 1964, Williams 1972).

Relative abundance data are in general agreement with most previous studies conducted in or near the study area (Rand 1964, Turner and Gist 1970, Schoener and Schoener 1971, Lister 1981), but differ from those of Moll (1978) who found *A. evermanni* to be relatively more abundant than *A. gundlachi* in similar habitat.

Because vertical surveys showed that *A. stratulus* is primarily a canopy species within the forest, the relative abundance data obtained here are chiefly of value in demonstrating the general homogeneity of the study area, providing baseline estimates for future studies, and relating present conditions to previous research.

b. The results of multiple mark and resight surveys of *A. stratulus* conducted at the tower are presented in Table 34. Reasonable numbers of recaptures and high recapture success produced relatively accurate population estimates. The three methods used to calculate population densities (Jolly-Seber, Manly-Parr, and Lincoln Index) provided similar estimates of 32.5, 32.0, and 35.0 lizards respectively (Table 35).

Table 33. Relative abundances of the three common anoline lizard species during wet and dry season surveys* at four randomly selected locations within the study area.

Transect No.	*Anolis gundlachi*		*Anolis evermanni*		*Anolis stratulus*	
	Wet	Dry	Wet	Dry	Wet	Dry
1	85%	59%	15%	36%	-	5%
2	84%	71%	16%	25%	-	4%
3	90%	69%	3%	25%	7%	6%
4	87%	57%	13%	26%	-	17%
Mean	86%	64%	12%	27%	2%	9%

*Wet Season = September 1980, Dry Season = January-March 1981

Table 34. Mark and resight data for dry season 1981 tower surveys.

Dates (1981)	FEBRUARY		MARCH	
	23	26	2	5
Total Sightings	25	17	20	21
Total Resighted	-	13	16	18
Percent Resighted	-	77%	80%	86%

Table 35. Population density estimates obtained by three standard methods for *Anolis stratulus* at the tower during the 1981 dry season (February - March).

Methods of Analysis	Population Estimates*	Average Estimates*	Population Density
Manly - Parr	28.3 ± 5.5 35.6 ± 11.4	32.0 ± 8.5	$2.5/m^2$
Jolly - Seber	29.0 ± 6.1 39.9 ± 11.4	32.5 ± 8.8	$2.6/m^2$
Lincoln Index	32.7 ± 8.6 34.0 ± 14.9 38.2 ± 15.6	35.0 ± 13.0	$2.6/m^2$

* Including 95% confidence interval

Because of the vertical orientation of the transect, it was a point sample with respect to areal density. Population densities were estimated on the basis of maximum (and alternatively the mean) sight and resight distances to lizards observed during surveys as the radius of a circle around the tower and dividing the population estimates by the area in square meters within this circle. Density estimates range from 2.5 to 7.0 lizards/m^2 (25,000 to 70,000 lizards/ha). Additional surveys are planned to obtain wet season estimates. In the meantime it is prudent to use the lower estimate until supporting data can be obtained. Even at that level (25,000/ha) it is the highest lizard population density known, exceeding the density estimates of 20,000/ha obtained for A. pulchellus by Gorman and Harwood (1977) at a nearby lowland site in eastern Puerto Rico.

The high densities appear to be the consequence of A. stratulus inhabiting home range territorial volumes layered within the canopy rather than subdividing the habitat on a strictly areal basis. Supporting evidence for this was obtained by recording the vertical range of movement of individually marked lizards which were observed a minimum of 10 times. Males, females, and juveniles all appear to confine their activities to a vertical range of five to six meters (Figure 15 and 16).

Although these overlapped considerably, none of these spanned the total vertical range of available habitat (10 to 22 m) in the forest canopy. Occasional movements outside the home range were usually toward ground level, accounting for the limited sightings of this species by ground-based observers. None of the lizards had home ranges extending below the 5 m level (Figures 15 and 16).

The high population density of A. stratulus in the forest indicates that the species is an important component of the diurnal food web and suggests that a considerable amount of foraging takes place in the forest canopy. Canopy foraging is also indicated by the gut analysis studies (section 5.4.1, Subtask 3). The high abundance of this insectivore suggests that it may play an important role in controlling herbivorous insect abundance in the canopy, thus playing a potentially significant role as a regulator species in the forest ecosystem (Glasser 1979).

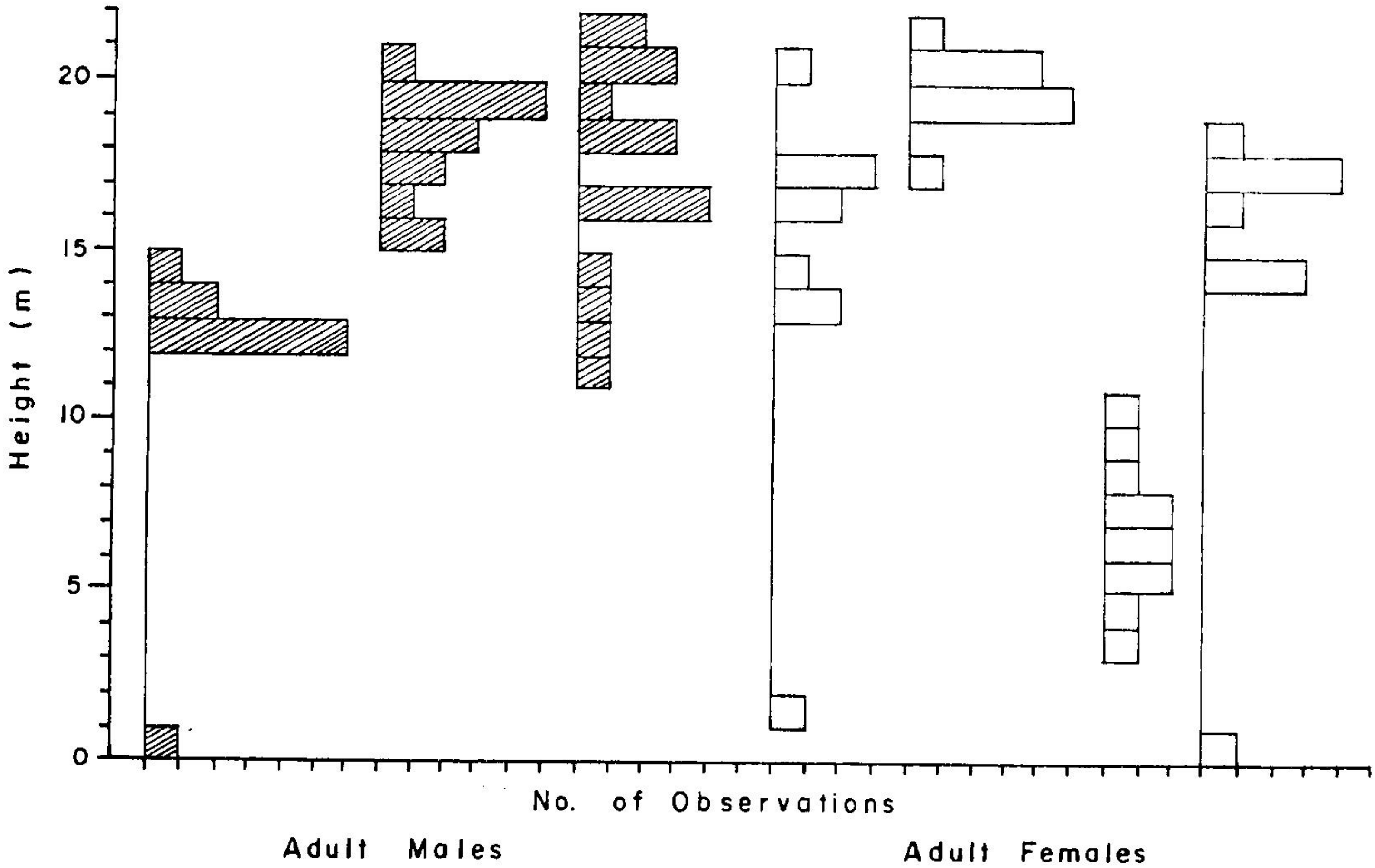


Figure 15. Vertical distribution of adult Anolis stratulus observed more than ten times at the tower (February - April 1981).

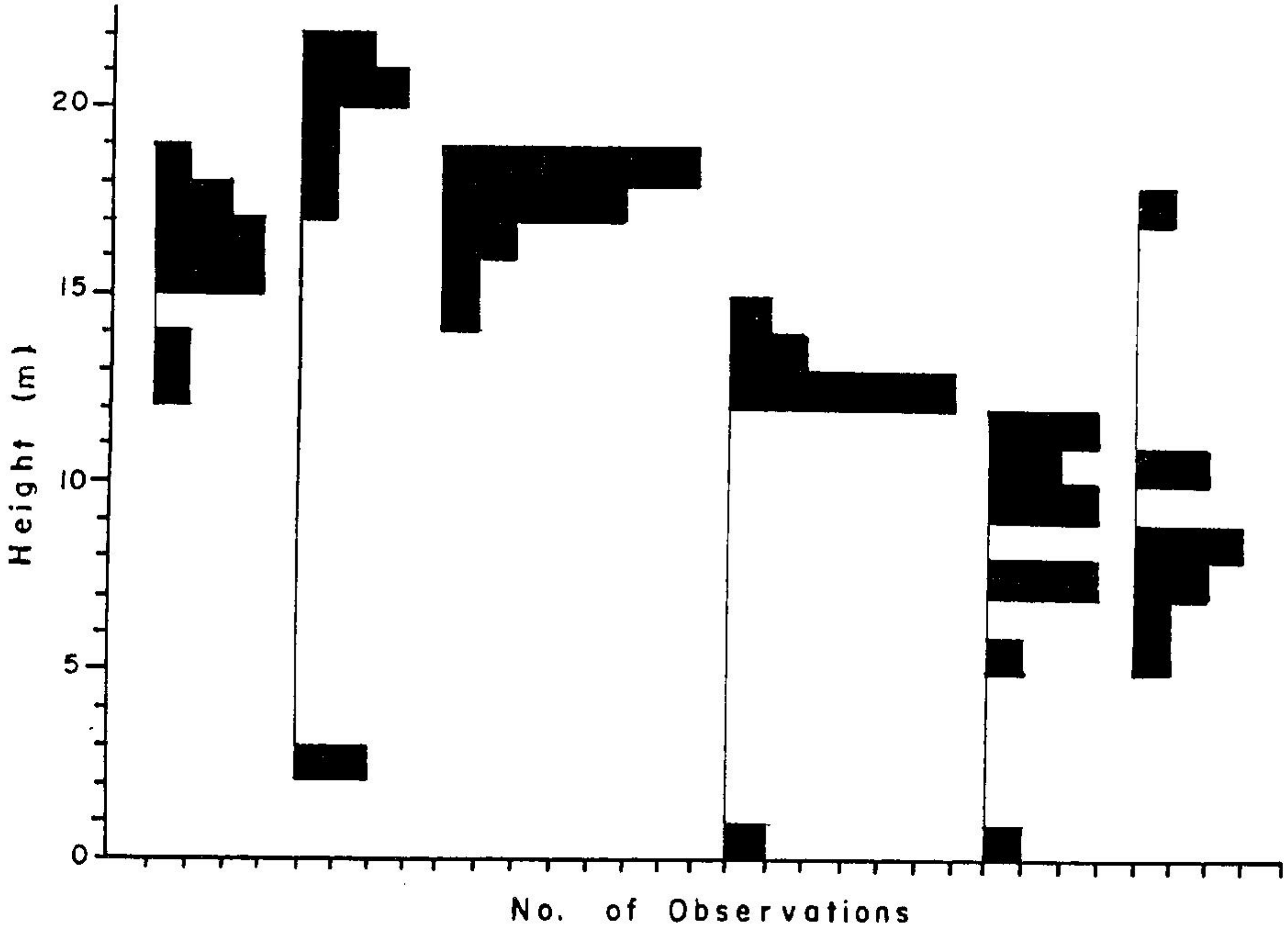


Figure 16. Vertical distribution of subadult *Anolis stratulus* observed more than ten times at the tower (February - April 1981).

Subtask 5. Vertical Distribution of Anoline Lizards

Surveys conducted at the tower demonstrated differences in vertical distribution among the three common forest anoles. Wet season (September - November) 1980 and dry season (January - March) 1981 results are presented in Figures 17 and 18.

Anolis gundlachi was rarely observed more than 5 m above ground level during either season. The few sightings made above this level were males and were made during the late afternoon, suggesting that these individuals may have been moving toward their night resting locations. The species is normally a trunk-ground forager which explains its confinement to the lower levels of the forest.

Anolis evermanni is distributed throughout the vertical extent of the forest, but appears to be more common at ground level. This may be due in part to the difficulty of detecting green lizards in the dense canopy foliage. Although seasonal differences in vertical distribution were not detected, data obtained from horizontal transect sampling at ground level (Subtask 4, section a) suggests that they may exist.

Anolis stratulus was found most abundantly in the forest canopy during both seasons. Only a small percentage (approximately 10%) of the total observations were below 5 m, the zone predominantly occupied by *A. gundlachi* and *A. evermanni*. Significant differences (p 0.05) were found between wet and dry season distributions using the Kolmogorof-Smirnoff test. During the wet season activity is concentrated within the canopy. During the dry season the vertical distribution is more dispersed into the high canopy and toward ground level. Preliminary gut analyses (Section 5.4.1, Subtask 3) indicate that less food may be taken at that season, suggesting that the change in distribution could be related to foraging. The majority of lizards observed below 5 m were females who may have been coming to ground level to deposit eggs. Previous researchers in the forest have been confined to ground level. Although some (Rand 1964, Lister 1981) have attempted to census lizards throughout the vertical extent of the forest, most observations have been made below 5 m. This is undoubtedly the result of poor light conditions, distance, and the fact that

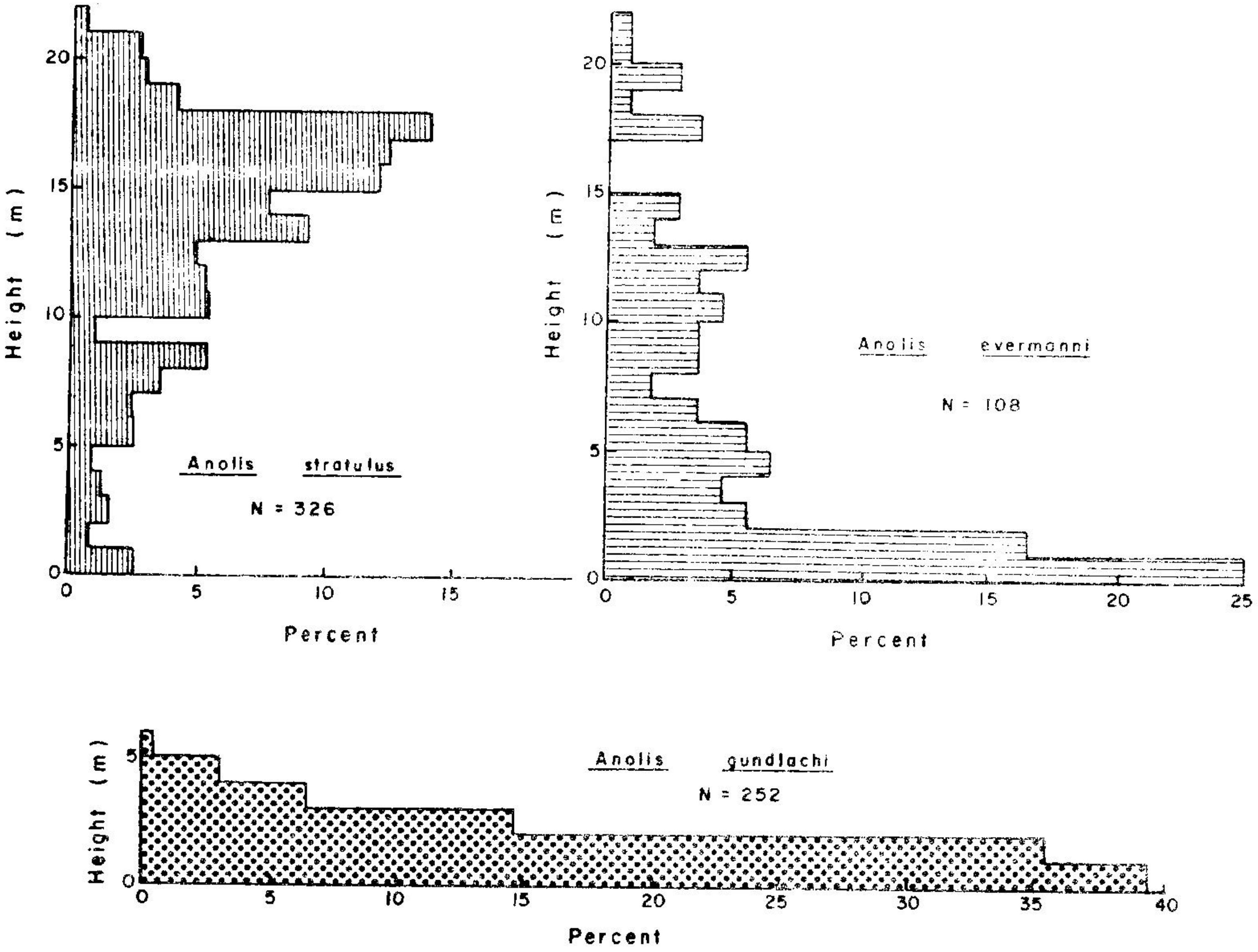


Figure 17. Vertical distribution of Anolis spp. during the wet season (September-November 1980).

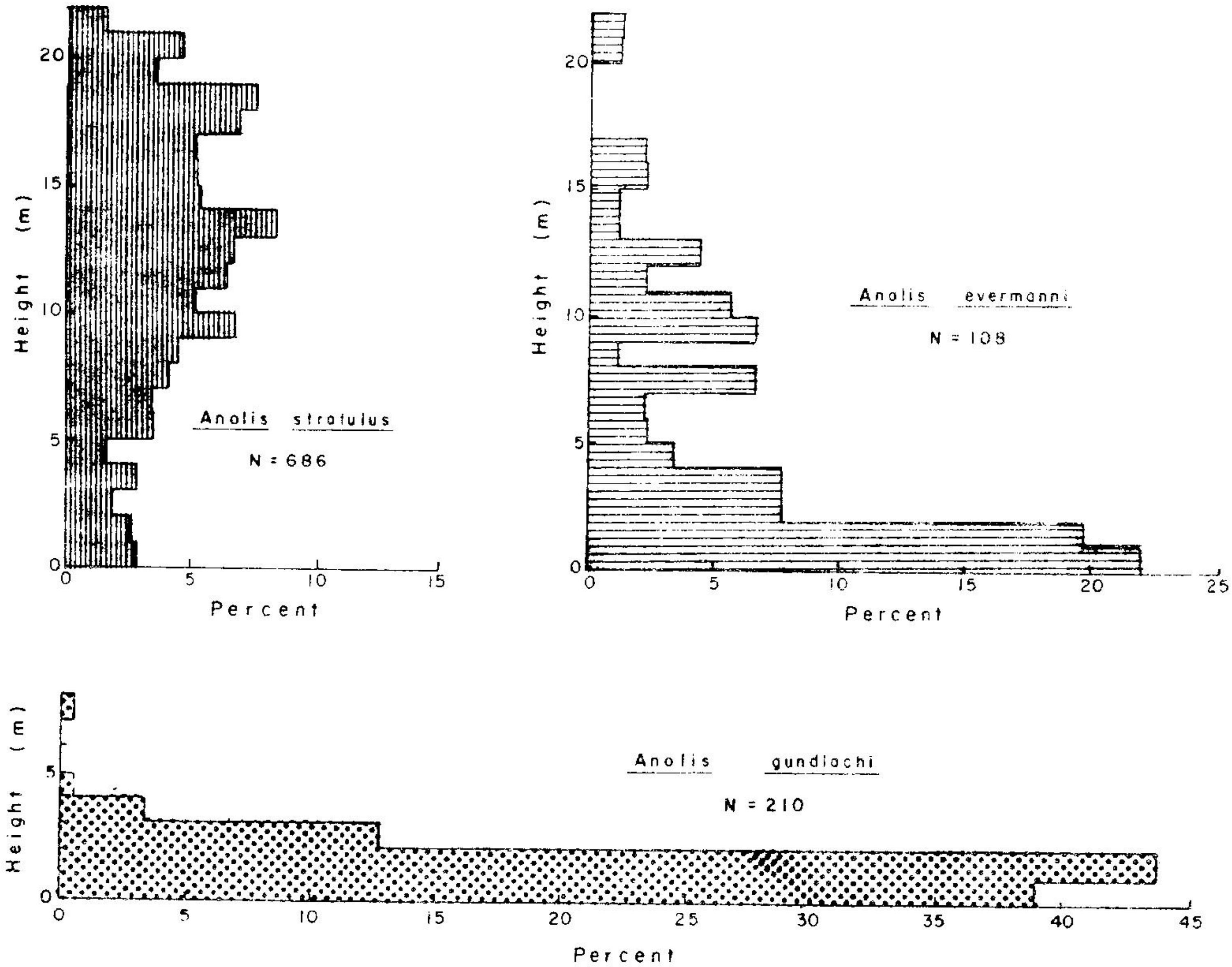


Figure 18. Vertical distribution of Anolis spp. during the dry season (January-March 1981).

many lizards in the canopy perch on the upper sides of branches and leaves and cannot be seen from below. These limitations have lead to the erroneous conclusion that most anoline lizards inhabit the lower few meters of the forest (Rand 1964, Lister 1981). Rand (1964) speculated that *A. stratulus* might occur high in trees but was unable to document this.

The discovery of *A. stratulus* as a canopy species present at high population densities (Subtask 4) is an important aspect of overall trophic organization. Vertical stratification as a means of habitat partitioning has been demonstrated for other lizard communities at other locations in the neotropics (Andrews 1971, Schoener 1968) in addition to the basic studies conducted in Puerto Rico (Rand 1964, Schoener and Schoener 1971). The discovery of *A. stratulus* as an abundant canopy species in the rain forest has important implications with respect to ecosystem trophic structure. The vertical stratification of lizard species indicates the probable significance of vertical structure in the overall food web, and provides additional information relevant to the controversy concerning the interrelationship between anoline lizards and insectivorous birds in West Antillean forests (Moermond 1981 in press, Wright 1981, Waide and Reagan 1982).

Subtask 6. *Anolis* Population Growth and Turnover Rates

Anolis stratulus branded during multiple mark and resight studies at the tower (Subtask 4, Section b) are providing information on the growth rate and population turnover of this species in the forest. Marked individuals will be recaptured periodically to obtain weight and length measurements for comparison with data collected at the time of initial capture. Population turnover data will be estimated by noting changes in the relative proportion of marked to unmarked individuals through time. Additional studies may be undertaken, but these are presently considered peripheral to the main thrust of Phase II research.

5.4.3 Birds

Subtask 1. Population Density

<u>Transect Counts</u> - Figures 19-21 show seasonal changes in population density for the 13 most common bird species at El Verde. Each graph represents the monthly sum of population densities calculated from sight, song and call detections and indicates a minimum density. Data from all plots were combined to estimate densities.

Figures 22-25 show separate population densities in each plot for four species common at El Verde. Densities calculated from detections by sight, song and call are shown on separate graphs in order to demonstrate seasonal fluctuations in population estimates that are due to changes in activity.

<u>Mist Nets</u> - Table 36 gives the number of individual birds captured in mist net surveys of plots 1-4 during September-October 1980. The Ruddy Quail-Dove was the species most commonly captured in all study sites and far out-numbered all other species except in plot 4. Samples from plots 2 and 4 had equal numbers of species (7), even though sample size was much greater in the former (31 and 11, respectively). The sample from plot 3 had 5 species and that of plot 1 had 4.

<u>Spot Maps</u> - Table 37 gives the results of spot map and transect censuses from June-July 1981. Plot 3 was contained within the gridded area used for spot mapping (see Figure 2). Densities from transect counts represent the greater of 1) double the number of singing males detected or 2) the sum of detections from sight, song and call (Emlen 1971). Thirteen species were found in spot mapping and only nine in transects, a result that is not unexpected considering the greater area (9.0 vs 7.2 ha) and amount of time (10 vs 2 days) spent in spot map counts. Population densities of two species (Stripe-headed Tanager and Puerto Rican Tanager) could not be determined in spot map censuses since these birds were not singing at the time of the counts.

Table 38 compares densities from spot map counts conducted by Recher (1970) in April-May, 1964-66, with transect censuses performed in April 1981 during the present study.

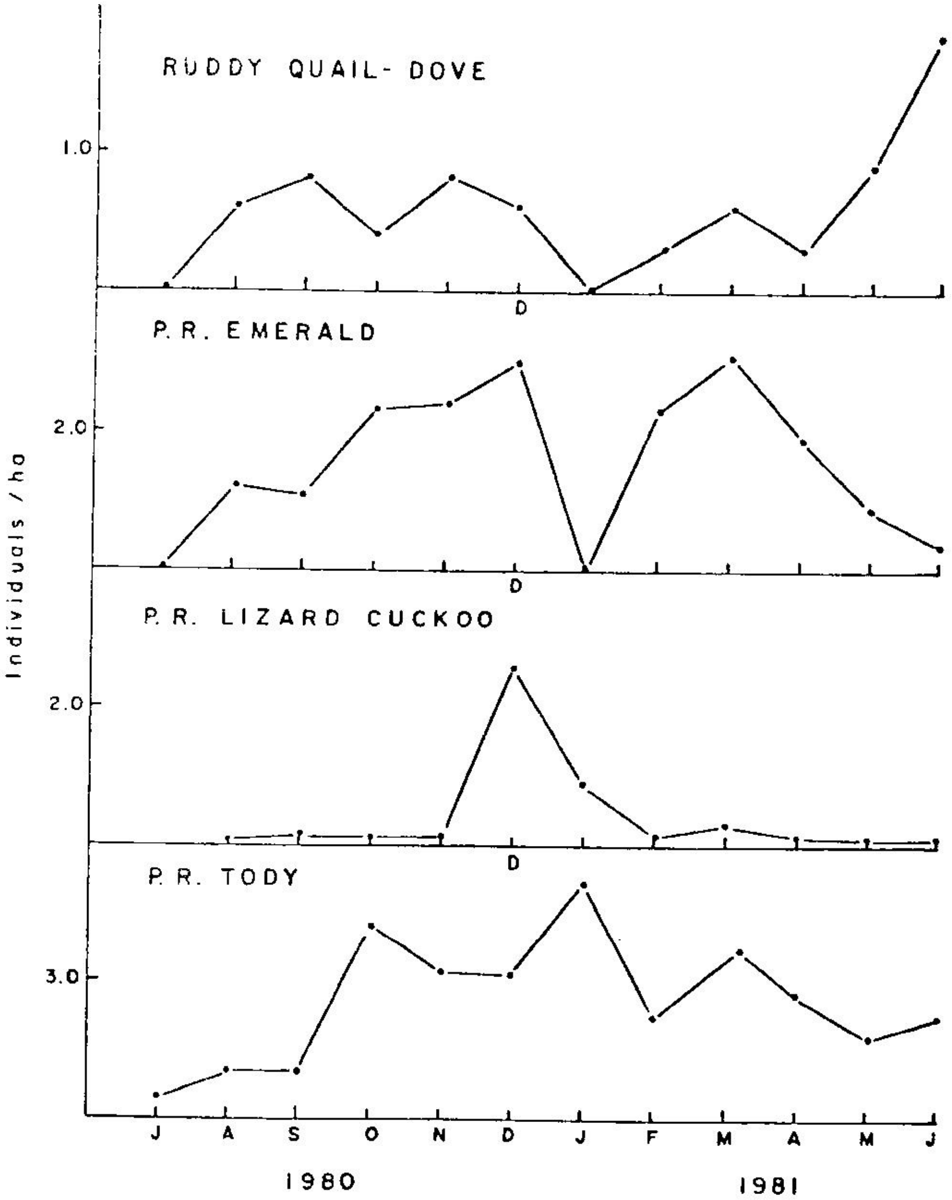


Figure 19. Seasonal changes in population densities from transect counts at El Verde.

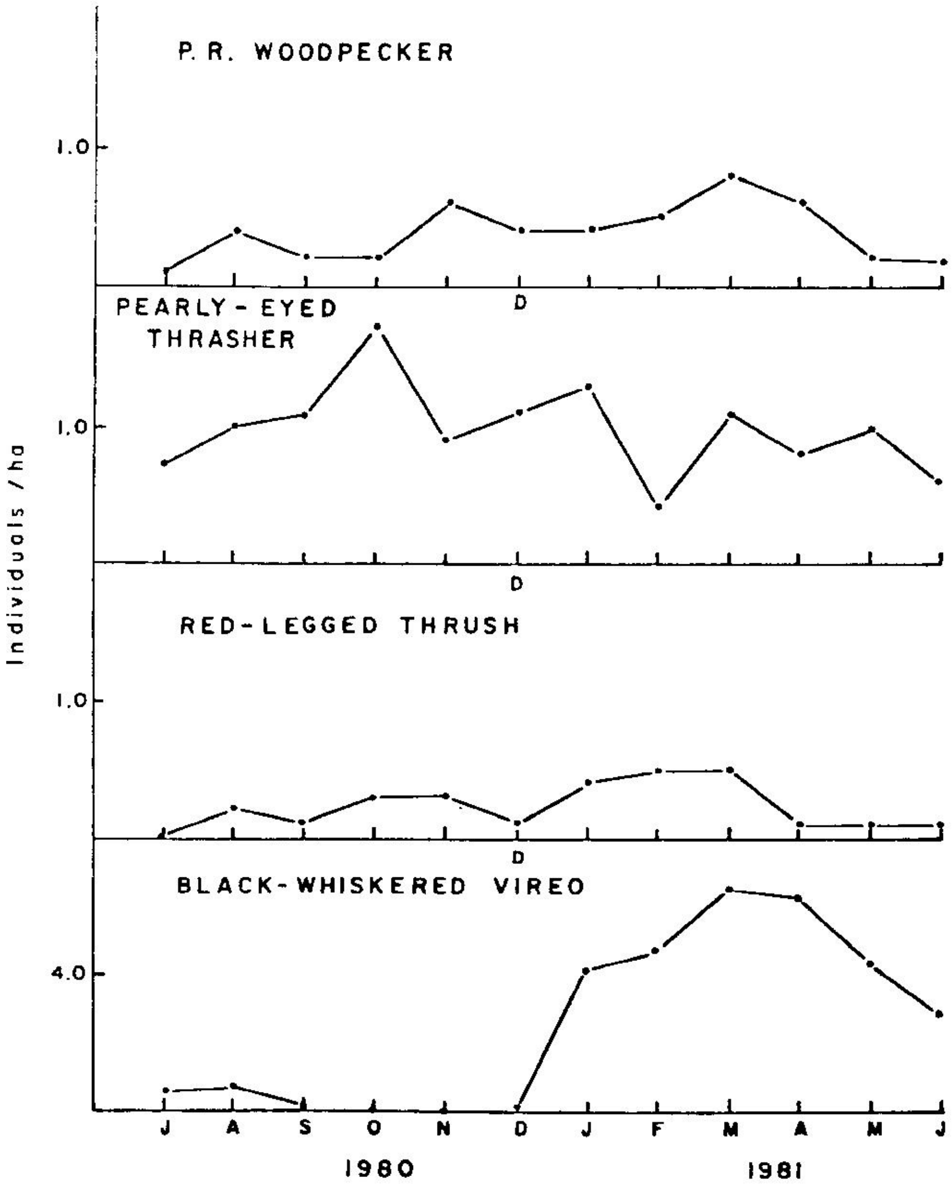


Figure 20. Seasonal changes in population densities from transect counts at El Verde.

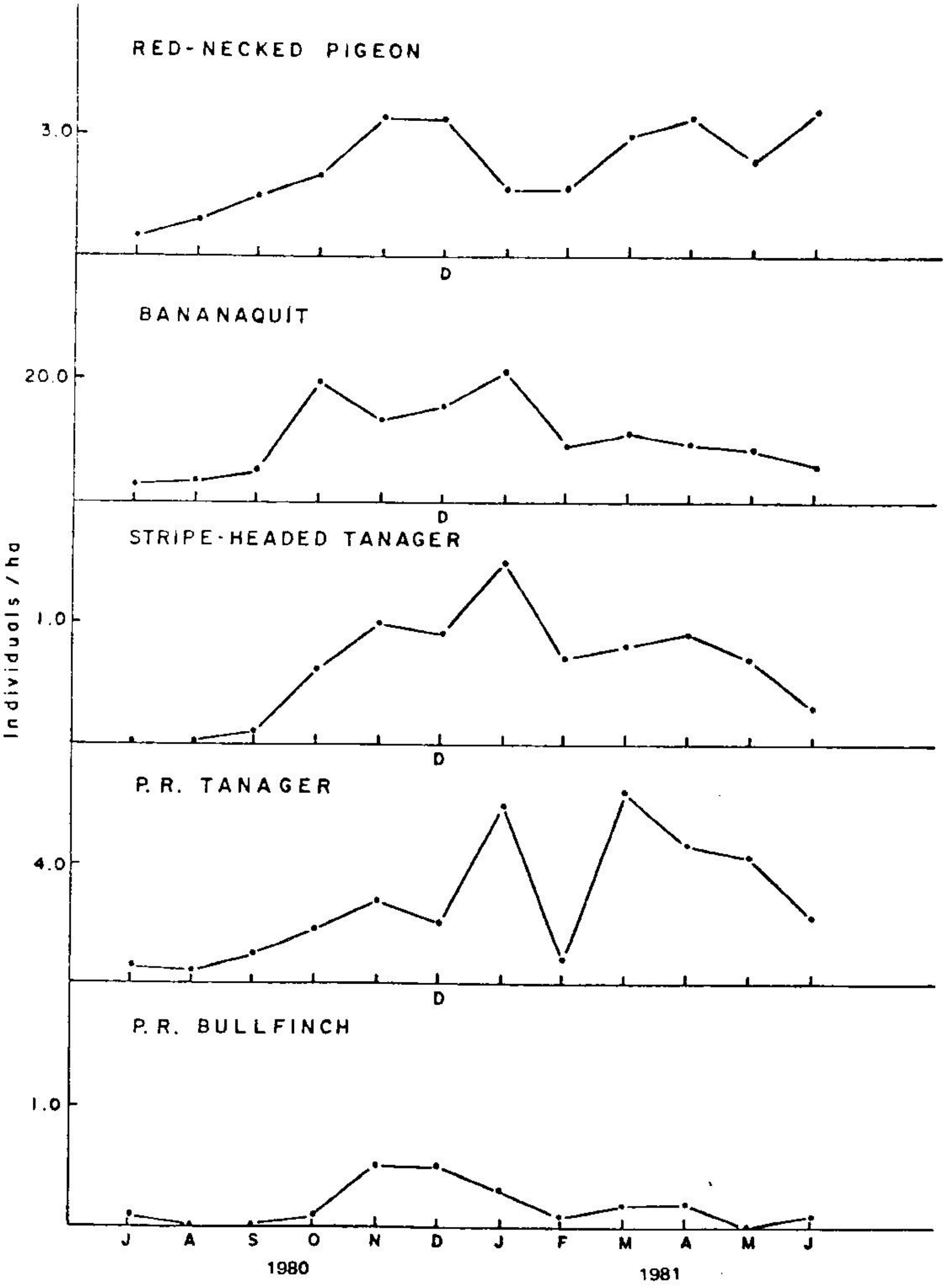


Figure 21. Seasonal changes in population densities from transect counts at El Verde.

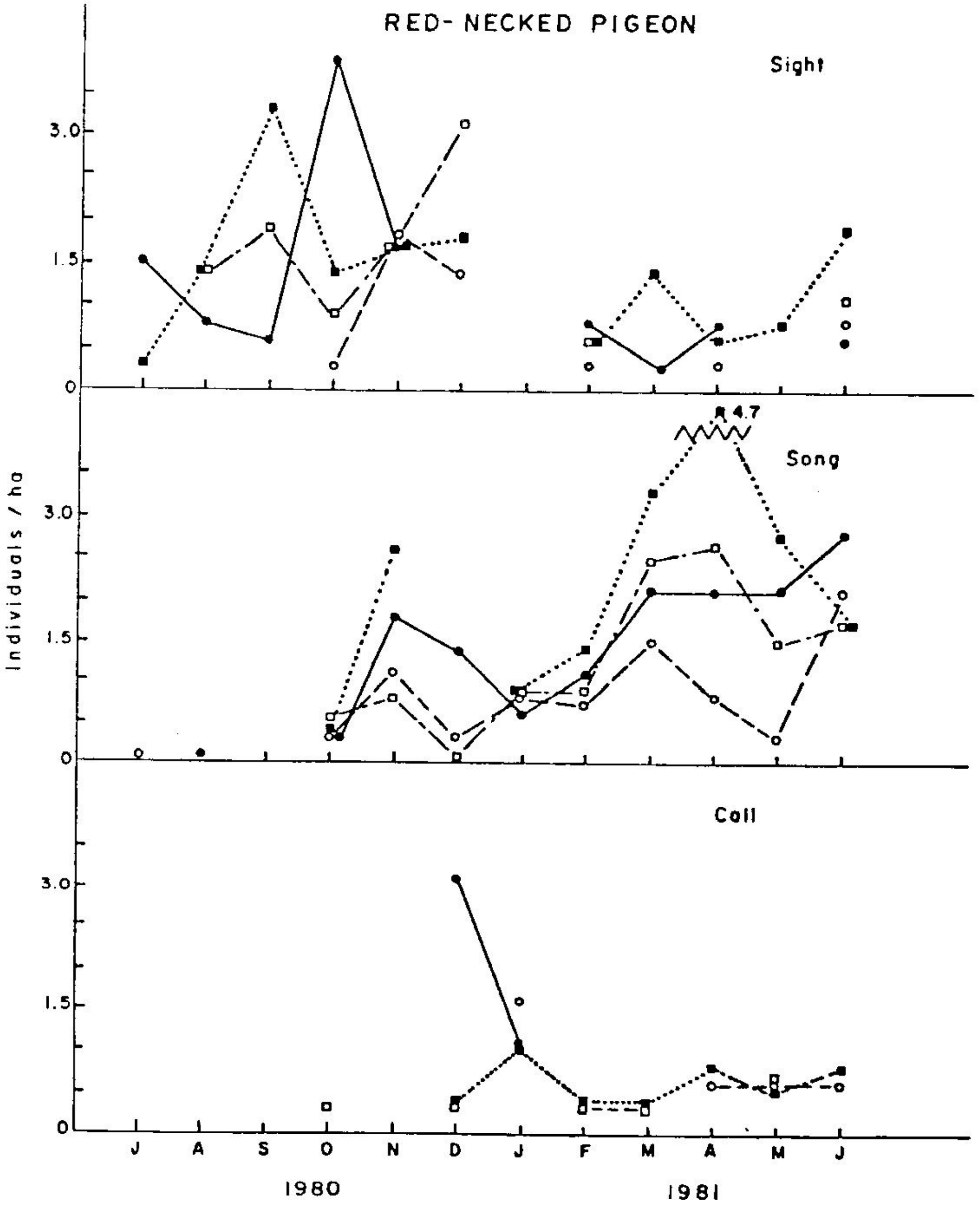


Figure 22. Seasonal changes in abundance of Red-necked Pigeons in four plots at El Verde. Plot 1 = (○ --), plot 2 = (● —), plot 3 = (□— -), plot 4 = (■·······).

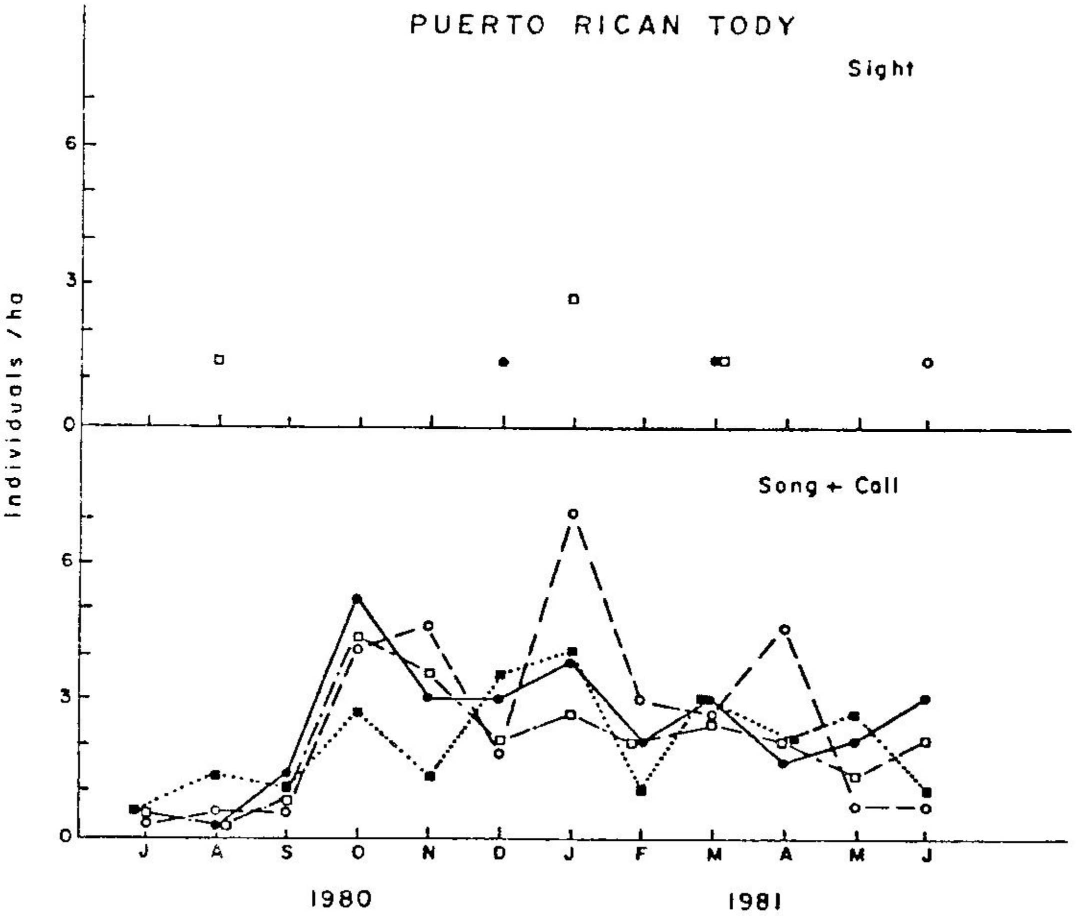


Figure 23. Seasonal changes in abundance of Puerto Rican Todies in four plots at El Verde. Plot 1 = (○ --), plot 2 = (●—), plot 3 = (□—-), plot 4 = (■······).

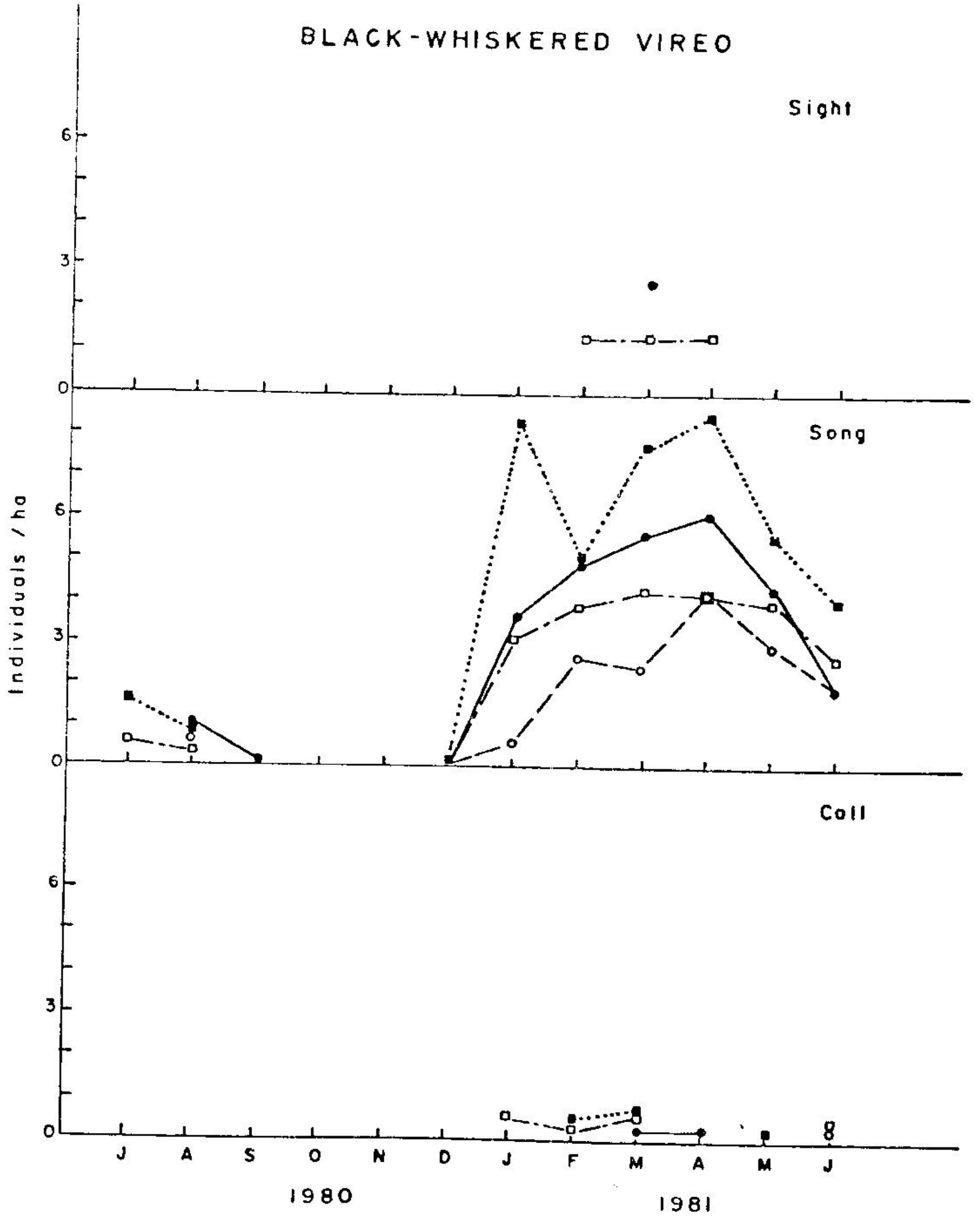


Figure 24. Seasonal changes in abundance of Black-whiskered Vireos in four plots at El Verde. Plot 1 = (○ --), plot 2 = (● —), plot 3 = (□ —·), plot 4 = (■ .....).

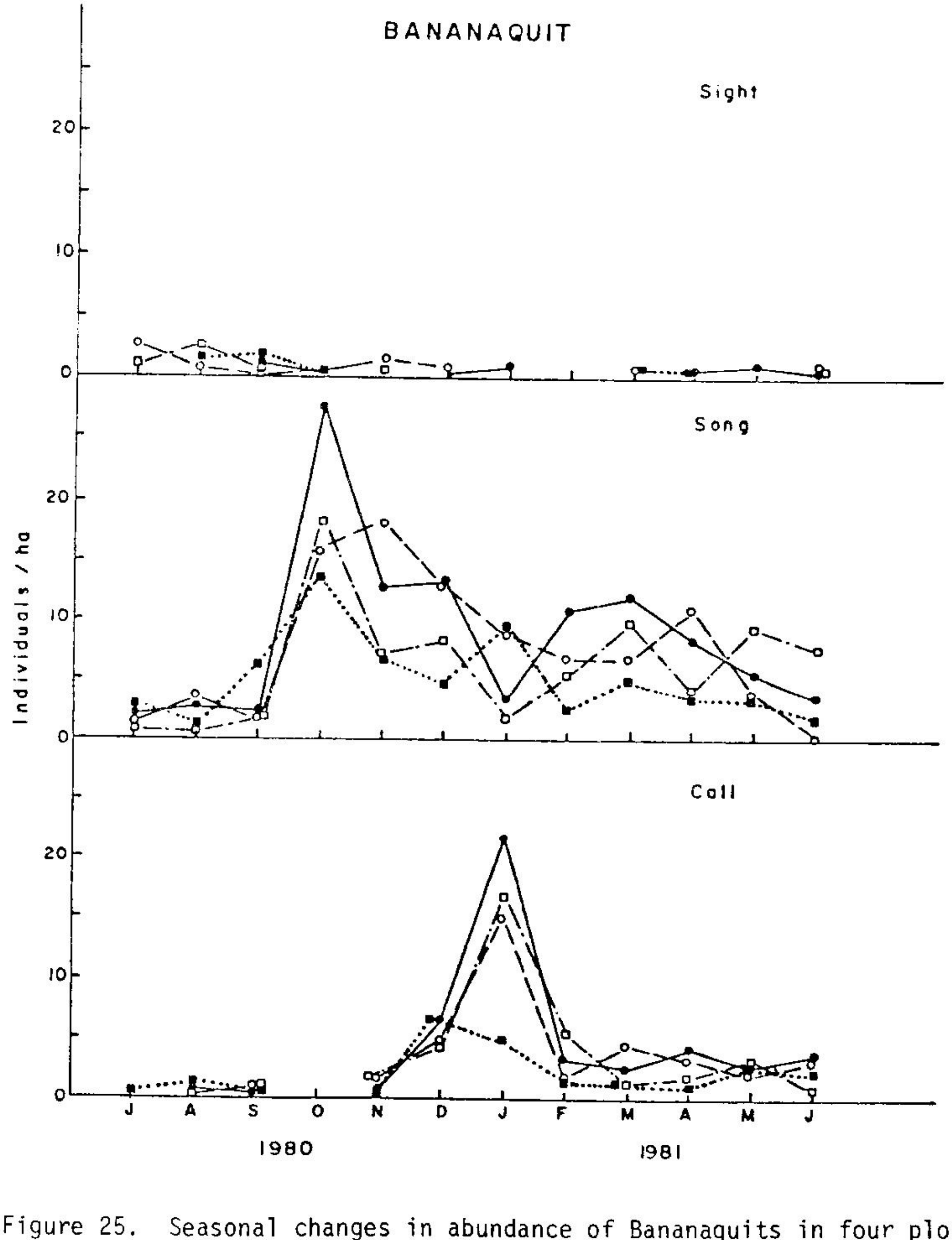


Figure 25. Seasonal changes in abundance of Bananaquits in four plots at El Verde. Plot 1 = (○ --), plot 2 = (● ——), plot 3 = (□ —), plot 4 = (■ ······).

Table 36. Number of captures and capture rate for various birds species in Plots 1-4.

	Plot 1	Plot 2	Plot 3	Plot 4	Total
Ruddy Quail-Dove	9	16	16	3	44
Puerto Rican Emerald	2	2	2	2	8
Puerto Rican Tody	0	2	7	1	10
Pearly-eyed Thrasher	1	2	2	0	5
Red-legged Thrush	0	0	0	1	1
Black-throated Blue Warbler	0	0	0	2	2
Ovenbird	0	0	1	1	2
Bananaquit	3	2	0	1	6
Stripe headed Tanager	0	1	0	0	1
Puerto Rican Tanager	0	6	0	0	6
Total captures	15	31	28	11	85
Number of nets	11	10	10	10	
Number of days	3	3	4	3	
Captures/net-day	0.45	1.03	0.70	0.37	

Table 37. Population estimates by territory mapping and line transect methods. Territory maps were made between 2 June and 13 July 1981 and transect counts between 22-29 June 1981. Number of territories is multiplied by 2 for females and divided by area sampled to get density. Transect densities are calculated following Emlen (1971).

	Territory Mapping		Transect 3	All Transects
	Territories/9 ha	Individuals/ha	Individuals/ha	Individuals/ha
Red-tailed Hawk	1.0	0.2	0.0	0.0
Ruddy Quail-Dove	5.5	1.2	0.6	2.0
Red-necked Pigeon	11.2	2.5	3.4	4.2
P.R. Lizard Cuckoo	0.0	0.0	0.0	0.2
P.R. Emerald	2.0	0.4	0.0	0.4
P.R. Tody	7.9	1.8	2.2	2.2
P.R. Woodpecker	2.0	0.4	0.0	0.4
Stolid Flycatcher	1.0	0.2	0.0	0.2
Pearly-eyed Thrasher	1.0	0.2	0.3	0.6
Red-legged Thrush	0.0	0.0	0.0	0.1
Black-whiskered Vireo	10.5	2.3	5.2	5.2
Bananaquit	21.9	4.9	15.0	6.6
Stripe-headed Tanager	not singing		0.8	0.3
P.R. Tanager	not singing		1.6	2.2
P.R. Bullfinch	1.2	0.3	0.2	0.2

Table 38. Comparison of population estimates from territory mapping (1964-66) and transect counts (1981) during April-May at El Verde. Data from 1964-66 from Recher (1970).

	INDIVIDUALS/HA			
	1964	1965	1966	1981
Puerto Rican Emerald	0.4	0.4	0.4	1.9
Ruddy Quail Dove	0.6	0.5	0.4	0.3
Red-necked Pigeon	0.4	0.3	0.3	5.2
Puerto Rican Tody	1.9	2.0	2.2	2.7
Pearly-eyed Thrasher	1.2	1.6	0.6	0.8
Bananaquit	13.3	12.0	8.8	13.2
Black-whiskered Vireo	3.3	3.0	1.8	11.6
Puerto Rican Tanager	0.7	1.0	0.8	4.7
Stripe-headed Tanager	0.2	0.2	0.2	0.9
Puerto Rican Bullfinch	0.6	0.8	0.2	0.4

Discussion

Absolute population densities are necessary to calculate elemental and energy storage and flow through the food web. Spot or territory maps are the most widely accepted method of determining absolute densities, but they suffer from the disadvantage that they are labor intensive and appropriate only during the breeding season. To monitor seasonal changes in populations or to compare different areas, a more rapid method such as transect surveys is often used to obtain relative densities. The best features of each technique can be exploited by calibrating transect surveys to a spot map count performed in the same location (Holmes and Sturges 1975). This approach has been used in this study.

Density Estimates

Comparison of spot maps and transects from the plot 3 (Table 37) reveals two general differences in density estimation. The transect survey misses several rare species (Hawk, Emerald, Woodpecker, Flycatcher) detected in spot mapping. This is most likely a result of the smaller sampling effort put into transect surveys and the lack of replication as these species were detected in other transects. The most abundant species (Bananaquit, Vireo, Pigeon, Tody) have densities that are higher measured by transect counts than by spot maps. The difference in this case cannot reflect the presence of juvenile birds toward the end of the breeding season since transect values for these four species were determined by doubling counts of singing adult males. A more likely explanation is that territorial birds sing less and have reduced site fidelity toward the end of the breeding season, resulting in a blurring of territorial boundaries and an underestimate by the spot map method. Spot map and transect counts will be repeated during the peak of breeding in 1982 to see if a closer agreement between the two methods is possible.

One of the problems of the spot map method is illustrated in Table 37. Not all species breed at the same time, and the effort required to perform spot map censuses precludes repeated sampling throughout the breeding season. Puerto Rican and Stripe-headed Tanagers were not breeding when the census was conducted and population estimates could not be made for these two species. Ruddy Quail Doves were singing vigorously at the time of the fcensus (see Figure 19) but all other species were less active than earlier in the breeding season. Spot map censuses must be carefully timed to sample as many species as possible.

Table 38 shows the results of spot map censuses conducted by Recher (1970) from 1964-66 and compares them to transect censuses from 1981. Six of the 10 species studied by Recher (Emerald, Quail Dove, Tody, Thrasher, Bananaquit, Bullfinch) have not changed appreciably in abundance, to judge by transects in April 1981 (Table 38) and spot maps and transects in June-July 1981 (Table 37). Three species (Hawk, Woodpecker, Flycatcher) did not appear in Recher's censuses but showed up in the 1981 counts. Four other species (Pigeon, Vireo, two Tanagers) were more abundant in 1981 censuses. Differences in abundance of the Puerto Rican Tanager between Recher's and the present study are due to the species' habit of travelling in large foraging flocks which results in extreme local fluctuations in abundance. Increases in calculated densities between 1964-66 and 1981 for the other three species reflect real increases in abundance during this period.

The general agreement between densities calculated from spot maps and transect censuses suggests that either technique is acceptable. Hence, transect densities will be used to calculate nutrient and energy storage. This practice has the advantage of allowing data from the peak breeding month for each species to be used to determine density at equivalent times in the breeding cycle. Whenever there is disagreement between transect counts and spot map censuses from the same month, a range of values will be given. For the Ruddy Quail Dove, mist net data suggest a higher density than calculated from other censuses, and this will be taken into account in the nutrient and energy calculations. No other species requires such special treatment.

Seasonal Density Changes - The trends shown in Figures 19-21 reflect seasonal changes in activity patterns as well as fluctuations in number. In general, birds are more conspicuous when defending territories, feeding fledglings, or foraging in post-reproductive flocks and less conspicuous during periods of incubation and molt. Despite the fact that seasonal trends are determined by changes in activity and abundance related to each species, a few general patterns are still apparent.

During July-September 1980, eight of the 13 species shown had their lowest densities of the year. This period follows the peak breeding for the avifauna as a whole (March-June; Recher 1970) and reflects a diminution of singing and territorial defense and reduced activity related to molt (Waide, unpublished data). For those species that breed only during the spring, the following months should show the greatest population size, although there may be local density fluctuations due to flocking and aggregations around food sources.

Seven of 13 species show their highest densities between December and March. This period reflects increased singing associated with territorial defense and the onset of reproductive activities. Exceptions to this general pattern are usually due to variations in breeding pattern. Ruddy Quail Dove density peaks in June-August (Recher 1970) during the main breeding period for this species. Bananaquits and Todies show less pronounced peaks extending over much of the year resulting from non-synchronized breeding in the former and year-round territoriality in the latter (Kepler 1977). The Red-necked Pigeon shows two peaks, the first (November-December) associated with aggregations of foraging birds in the plots and the second (March-June) due to singing males. The density of Pearly-eyed Thrashers shows only a small peak in October as a result of similar activity patterns throughout the year.

Seasonal changes in density for four common species are shown in Figures 22-25. Data from each plot and for sight, song and call detections are shown separately. Each of the four species represents a different pattern of seasonal density fluctuation based on differences in reproduction and foraging.

The Red-necked Pigeon shows a single peaked curve for detections by song, with all four plots showing maxima between March and June (Figure 22). Many birds were sighted from September-January in aggregations around fruiting trees resulting in the double-peaked curve of Figure 21. These birds are shy and flush noisily at the approach of an observer and as a result most birds in the census area are detected even when they are not vocalizing. Maximum densities of sighted birds in the fall are about the same magnitude as those of singing birds in the spring (1.5-4.0 birds/ha) but fall densities fluctuate greatly as birds move between transient fruit sources. The species can be characterized as having a sychronous breeding season with habits that make it conspicuous during the rest of the year.

The Puerto Rican Tody (Figure 23) is an inconspicuous understory bird that is seldom seen without being heard first. The Tody occupies territories in pairs year-round and both sexes vocalize (Kepler 1977). As a result, densities are fairly uniform throughout the year with minor peaks in October, January, and March. Densities decline in the spring as the activity of adults is centered around the nest burrow. Seasonal abundance patterns for all four plots are similar. The species can be characterized as having permanent territories with synchronous breeding (April-July, Kepler 1977).

The Black-whiskered Vireo is the only Puerto Rican land bird to migrate from the island after breeding. Singing activity shows a plateau during February-April (Figure 24). It is noteworthy that density values for the different plots maintain a constant relationship throughout the breeding season, with plot 4 having the most individuals and plot 1 the fewest in all months. The species has synchronous breeding and is a summer resident.

The Bananaquit's extended breeding season is reflected in the prolonged singing activity seen in Figure 25. A pronounced peak in song occurs in October-November and is followed by a peak in calling individuals (fledglings begging?) in January. Biaggi (1955) states that Bananaquits nest throughout the year, but Figure 25 suggests some seasonality in breeding activity. Wetmore (1927) also found the species to breed year-round with most occupied nests occurring between February and June. The species can be described as having asynchrous breeding with multiple broods.

Subtask 2. Feeding Behavior

Figure 26 shows the proportion of observations at different heights for 10 common species at El Verde. The species are arranged

Figure 26. Foraging heights of 10 common bird species at El Verde.

so that members of the same trophic level are adjacent for easy comparison. Hence, nectarivores (Emerald and Bananaquit), vertebrate predators (Lizard Cuckoo), frugivore/granivores (Pigeon and Quail-Dove), insectivores (Tody), omnivores (Vireo and Tanager), and frugivores (Tanager, Thrasher and Thrush) are all grouped together.

Preliminary foraging data are summarized in Table 39. Field work in this subtask is still underway and will be augmented by 2800 unpublished foraging observations by Cameron and Angela Kepler and information from the literature.

Discussion

Data from Phase I studies can be used to give a preliminary idea of feeding behavior. Accumulation of information under this subtask is still underway and will continue in Phase II.

Only two species, the Puerto Rican Emerald and the Bananaquit, have been observed to take nectar in their diet (Table 39). The Bananaquit forages from ground height to the canopy, but concentrates on mid-levels. The Emerald specializes on undergrowth flowers (Figure 26). The Puerto Rican Lizard Cuckoo, a predator specializing on reptiles and amphibians (Wetmore 1916), ranges throughout the forest. The Puerto Rican Tody, an insectivore, forages principally under 10 m while the Black-whiskered Vireo takes both insects and fruit above 10 m. The Puerto Rican Tanager also consumes both fruit and insects but ranges more widely in the forest. Two columbids take both fruit and seeds, but one (Red-necked Pigeon) specializes on the fruits of canopy trees while the other (Ruddy Quail-Dove) searches for fallen fruits and seeds on the ground. All of the pairs or trios mentioned show at least some vertical stratification between one another.

Among other frugivores the situation is quite different. The Pearly-eyed Thrasher and Red-legged Thrush consume mostly fruit (Wetmore 1916) and overlap broadly in their vertical distribution. The Thrush is less common in dense forest and occurs more often on the ground where the Thrasher is never found. Insufficient data exist for the rarer frugivores (Puerto Rican Woodpecker, Stolid Flycatcher, Stripe-headed Tanager, Puerto Rican Bullfinch) to describe their foraging behavior.

Table 39. Preliminary data on diet of 14 bird species.

	Number of Observations			
	Fruit	Insect	Nectar	Lizard
Red-necked Pigeon	2	0	0	0
P.R. Lizard Cuckoo	0	0	0	1
P.R. Emerald	0	5	23	0
P.R. Tody	0	33	0	0
P.R. Woodpecker	0	1	0	0
Stolid Flycatcher	0	3	0	0
Red-legged Thrush	3	1	0	0
Black-whiskered Vireo	0	4	0	0
Black-and-white Warbler	0	1	0	0
Black-throated Blue Warbler	0	12	0	0
Parula Warbler	0	3	0	0
American Redstart	0	2	0	0
Bananaquit	1	10	10	0
P.R. Tanager	5	12	0	0

Subtask 3. Diet and Weight

Table 40 gives the number of birds color-banded during population studies and the number of stomach samples obtained to date from sacrificed birds and emetic chemicals. Analysis of stomach samples is underway to augment foraging observations in describing diets for each species. The comprehensive study by Wetmore (1916) and monographs on the Bananaquit (Biaggi 1955), Red-legged Thrush (Rolle 1965), and Puerto Rican Tody (Kepler 1977) provide basic material for structuring the food web.

Tables 41-42 give sample sizes, means and their standard errors for weight, wing chord, tarsus length, and bill length, depth and width for birds caught in Phase I studies. Whenever possible, male and female-plumaged birds are shown separately.

The weights given in Table 41 will be used to calculate nutrient and energy storage upon completion of the elemental analysis. Each bird collected was plucked and the proportion of body weight in feathers and tissue was determined as were dry and wet weights for each component. This information will be used to calculate storage in the avifauna and nutrient and energy turnover due to molt and population turnover.

Subtask 4. Materials Discharge

Because of difficulties in perfecting methodologies for collecting feces from caged birds without contamination, this subtask has not been completed. Changes in experimental design will be implemented in Phase II and will lead to completion of this task at an early date.

Subtask 5. Elemental Content

Forty-five individuals of nine bird species were collected and analyzed under this subtask. In addition, some fruits commonly found in the diets of birds have also been analyzed. Results of these analyses are presented in 5.2.1.

5.4.4 Mammals

No mouse-sized mammals were trapped in 80 trap nights, and none

Table 40. **Number of birds** color-banded and number of stomach samples obtained in Phase I.

	Number of birds banded	Number of stomach samples
Ruddy Quail-Dove	65	8
Green Mango		1
P.R. Emerald		7
P.R. Tody	23	7
P.R. Woodpecker		1
Pearly-eyed Thrasher	9	4
Red-legged Thrush	9	13
Black-whiskered Vireo	7	3
Bananaquit	47	8
P.R. Tanager	39	20
P.R. Bullfinch	4	3
TOTAL	203	75

Table 42. Means and their standard errors for bill length, bill depth and bill width of birds caught in Phase I. Birds in immature plumage and females are lumped in (♀).

		Bill Length (mm)			Bill Depth (mm)			Bill Width (mm)	
	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.	n	$\bar{x}$	S.E.
Ruddy Quail-Dove ♀	24	7.4	0.10	24	4.40	0.064	24	3.59	0.097
♂	34	7.5	0.09	34	4.56	0.055	34	3.59	0.078
Green Mango	2	23.5	0.92	2	2.29	0.025	2	3.14	0.555
P.R. Emerald ♀	13	12.8	0.25	13	1.74	0.035	13	2.34	0.052
♂	7	12.0	0.31	7	1.97	0.156	7	2.37	0.112
P.R. Tody	11	13.2	0.27	11	3.04	0.054	10	4.71	0.067
P.R. Woodpecker	1	19.2	-	1	6.50	-	1	6.98	-
Pearly-eyed Thrasher	11	18.2	0.22	11	8.81	0.220	11	7.33	0.161
Red-legged Thrush	12	16.4	0.31	12	7.12	0.137	12	6.80	0.140
Black-whiskered Vireo	4	11.0	0.09	4	4.89	0.078	4	4.59	0.088
Black-throated Blue Warbler	1	7.2	-	1	2.95	-	1	3.43	-
Louisiana Waterthrush	2	10.8	0.27	2	4.29	0.030	2	4.16	0.265
Ovenbird	1	8.9	-	1	4.23	-	1	4.47	-
Bananaquit	28	10.4	0.15	27	3.65	0.039	27	3.68	0.053
Stripe-headed Tanager	1	8.1	-	1	7.09	-	1	7.00	-
P.R. Tanager	23	11.7	0.17	23	7.90	0.066	23	7.07	0.064
P.R. Bullfinch	4	10.8	0.45	4	11.23	0.453	4	8.74	0.733

have been observed in rain forest habitat in the vicinity of the El Verde Field Station. The common house mouse (Mus musculus) is found near dwellings and in drier habitats elsewhere in Puerto Rico, but apparently is restricted from wetter areas.

Both the black rat (Rattus rattus) and Indian mongoose (Herpestes auropunctatus) were live-trapped within the study area. Two mongooses and 23 rats were trapped during a total of 175 trap nights and 150 trap days for trap success rates of 1.3 percent and 13.1 percent respectively. These results are consistent with general observations of both species. The Indian mongoose is occasionally seen foraging during the day, but the black rat is commonly observed on vines and in trees at night. The rain forest appears to be marginal habitat for the mongoose which reaches much higher densities in grassy and brushy lowland habitats in Puerto Rico and elsewhere in the West Indies (Seaman 1952, Pimentel 1955, Seaman and Randall 1962).

Three species of bats were captured during field surveys. Artibeus jamaicensis, a large frugivorous species, was the common species netted. Stenoderma rufum, a small frugivore, and Monophylla redmani, a nectarivorous species were less common. Artibeus was captured only in forest openings and usually at a height of several meters while the other two species were captured only in horizontal nets less than two meters above the ground and within the forest. A fourth species, Erophylla bombifrons, is also reported from the El Verde rain forest (Tamsitt and Valdivieso 1970) but was not captured during our field studies.

Abundance estimates were not obtained for any mammal species. The black rat and large fruit bat (Artibeus jamaicensis) are potentially important species in the movement and storage of energy and nutrients through the animal community because of their relatively large size, high metabolic rate (compared to the more abundant poikilotherms), and probable high biomass.

6.0 INTEGRATION

Nutrient cycling and energy flow are basic processes which characterize all ecosystems (Mason 1977). Solar energy is the ultimate force which drives energy flow, and energy is dissipated from the system without being recycled. Nutrients, however, cycle among ecosystem components. Inputs and outputs of many nutrients (elements and simple compounds) can be large or small, and their magnitudes in major ecosystem compartments (Figure 1) may directly influence ecosystem structure. Reciprocally, the storages in different compartments influence overall fluxes. It therefore follows that external factors which alter energy flow and elemental input or directly change compartment sizes may have a profound impact on overall ecosystem structure and processes.

We are attempting to develop a comprehensive description of ecosystem structure and function in terms of compartments and principal pathways of movement among them in order to understand how tropical rain forests might be affected by exogenous influences. Potential impacts resulting from energy development are being emphasized. This first phase of the Rain Forest Cycling and Transport Program has focused on expanding the information needed to elucidate these patterns and processes for the rain forest ecosystem near El Verde, Puerto Rico. The following sections consider the status of our present knowledge of cycling and transport processes, describe aspects of ecosystem organization relevant to these processes, and discuss the need for additional research on specific portions of the ecosystem.

6.1 Ecosystem Organization

A greatly expanded although largely qualitative food web description was developed in Phase I (Table 43). Given existing food web complexities only a few selected pathways could be quantified for energy flow and nutrient transfer. We have identified many of the major taxonomic groups comprising the several consumer levels and analyzed samples for elemental composition and caloric content. With few exceptions, chemical values do not differ greatly from those established for related taxa from other biotic regions.

Table 43. Key species and species groups in the trophic structure of the El Verde rain forest which were identified in Phase I.

	PRIMARY CONSUMERS		
Vertebrates:			
Mammals	bats (*Artibeus jamaicensis*), rats (*Rattus rattus*)	-	fruits and seeds
Birds	Ruddy Quail Dove (*Geotrygon montana*), Red-necked Pigeon (*Columba squamosa*), Red-legged Thrush (*Mimocichla plumbea*)	-	fruits and seeds
	Bananaquit (*Coereba flaveola*), Puerto Rican Emerald (*Chlorostilbon maugaeus*)	-	nectar
Invertebrates:			
Insects	Pumace fly larvae (Drosophilidae)	-	fruits and seeds
	leaf hoppers (Cicadellidae), plant hoppers (Fulgoroidea), walking sticks (Phasmatidae), crickets (Gryllidae), moth larvae (Noctuidae, Arctiidae, Microlepidoptera)	-	leaves
	Honey Bees (*Apis mellifera*), moths (Noctuidae, Arctiidae, Sphingidae), butterflies (*Dismorphia spio*)	-	nectar
snails	Giant Puerto Rican Land Snail (*Caracolus caracolla*)	-	leaves
	SECONDARY CONSUMERS		
Vertebrates:			
Birds	Puerto Rican Tody (*Todus mexicanus*)	-	insects
Reptiles	lizards (*Anolis stratulus*, *Anolis gundlachi*)	-	insects, snails, lizards

Continued table 43.

Amphibians	arboreal frogs (Eleutherodactylus coqui)	-	insects, snails
Invertebrates:			
Arachnids	pseudoscorpions (Menthus sp.), tailless whip scorpions (Phrynus palmatus), spiders (Theraphosidae, Uloboridae, Pholcidae, Araneidae, Ctenidae, Sparassidae)	-	insects, small invertebrates
	mites (Acarina)	-	animal parasites
Centipedes	Giant Centipede (Scolopendra alternans)	-	insects, small invertebrates
Insects	beetles (Staphylinidae)	-	insects, small invertebrates
	biting gnats, (Ceratopogonidae), mosquitoes (Culicidae), bots (Calliphoridae), tachinid flies (Tachinidae), parasitic wasps (Chalcidoidea, Scelionidae)	-	invertebrates and vertebrate parasites
	TERTIARY CONSUMERS		
Vertebrates:			
Birds	Puerto Rican Lizard Cuckoo (Saurothera vieilloti), Red-tailed Hawk (Buteo jamaicensis)	-	lizards, rats, centipedes
Reptiles	lizards (Anolis stratulus, A. gundlachi)	-	insects, frogs, lizards
	Snakes (Alsophis portoricensis)	-	lizards, frogs
Amphibians	arboreal frogs (Eleutherodactylus coqui)	-	insects, snails, frog eggs
Invertebrates:			
Arachnids	Tarantulas (Cyrtophilos portoricae), giant crab spiders (Olius spp.)	-	predatory insects

Continued table 43.

	tailless whip scorpions (*Phrynus palmatus*)	-	lizards, frogs
Centipedes	Giant Centipedes (*Scolopendra alternans*)	-	predatory insects, lizards, frogs

MACRODECOMPOSERS

Invertebrates:			
Arachnids	mites (Oribatidae and other families)	-	detritus
Crustaceans	sow bugs (*Philocia richmondi*)	-	detritus
Springtails	springtails (Entomobryidae)	-	detritus
Insects	termites (*Nasutitermis costalis*), crane fly larvae (Tipulidae), moth fly larvae (Psychodidae), biting midge larvae (Ceratopogonidae) midge larvae (Chironomidae), dark-winged fungus gnats larvae (Sciaridae), fungus gnat larvae (Mycetophilidae), gall midge larvae (Cecidomyiidae), soldier fly larvae (Stratiomyidae), ants (Formicidae)	-	detritus
Millipedes	millipedes	-	detritus

The primary producer level was evaluated as a compartment by estimating litterfall within the study site, evaluating previously unpublished data collected in the same area, and by consulting published information (see section 5.3). Similarities among different years and among different plots at the same site indicate site homogeneity at the chosen sampling scale (1 ha) and suggest a uniformity in annual litterfall rates. Seasonal variation was detected and is an important aspect of energy and nutrient transfer from the producer to the decomposer compartment even in the relatively aseasonal rain forest environment.

The primary consumer compartment (herbivores) differs in taxonomic composition from that found in comparable mainland forests (Fittkau and Klinge 1973). While insects are still prominent herbivores, monkeys and native rodents are entirely absent, bats are relatively important, there are no predominantly herbivorous reptiles, and the insect order Homoptera (planthoppers and leafhoppers) is substantially more important at El Verde than in the Amazon rain forest. Table 43 lists major species and taxonomic groups in the food web of the El Verde Forest. An introduced species, the roof rat, is the only rodent in the forest, but its importance as a primary consumer has not been determined. Herbivory by vertebrates is almost exclusively limited to fruits, seeds, and nectar, thus influencing the ecosystem by seed dispersal and pollination rather than by direct grazing.

Reliable estimates of the biomass of herbivorous arthropods have not yet been obtained, but preliminary sampling indicates that closely related taxa tend to be vertically stratified. Planthoppers and leafhoppers (sucking insects) are more abundant in the canopy than near ground level (section 5.4.1) Rates of herbivory have not yet been estimated, but in view of the substantial biomass of insectivorous predators supported by herbivorous arthropods, the rates are probably quite substantial.

Higher order consumers (secondary and above) are complexly interrelated in the food web. Arboreal frogs (Eleutherodactylus spp.) and anoline lizards (Anolis spp.) are the dominant secondary consumers. Unlike comparable mainland rain forests, large carnivores (e.g. jaguars) are not present. Several insect groups and other large arthropods (e.g. tarantulas, centipedes, tailless whip scorpions, etc.) are prominent predators.

In spite of the lack of quantification for many ecosystem compartments, important species and significant aspects of the food web were identified. Feedback loops exist in which large invertebrates (e.g. crab spiders) feed on small vertebrates (arboreal frogs) while the larger arboreal frogs eat small crab spiders (Formanowicz et al. 1981). Vertical stratification is also an important characteristic of foraging patterns within closely related taxa (e.g. anoles). Arboreal frogs and anoles, in spite of their small individual size, constitute a significant portion of total consumer biomass because of their extreme abundances (see section 5.4.2). Parallel day and night food subwebs are both important in terms of nutrient and energy movement between producer and consumer and between primary consumer and secondary consumer compartments. This partitioning of the overall food web is incomplete, but supports the basic concept of food subwebs in tropical ecosystems (Gilbert 1980).

The decomposer level remains the least known, both in terms of taxonomic composition and in terms of biomass. Macroarthropod decomposers include mites, crustaceans, millipedes, springtails, and a variety of insects. Termites, millipedes, springtails, and ants are abundant, but reliable estimates of biomass, population turnover rates, and numbers have not yet been obtained. Decomposition field studies focused on the pathway from producers to decomposers because of its quantitative importance. The role of soil fauna, especially large oligochaetes (earthworms), was not addressed during Phase I. Fittkau and Klinge (1973) estimate that as much as one half of the total animal biomass in their Amazon rain forest study area was soil fauna. If our study site is comparable in terms of macrodecomposers, earthworms are probably also important in the forest at El Verde.

6.2 Phase II Research

Information acquired in Phase I has contributed substantially to an understanding of cycling and transport processes, and has also provided a basis for determining the scope and emphasis of Phase II investigations. Major taxonomic groups in each ecosystem compartment (Figure 1) have been identified (Tables 43 and 44), but quantitative data on their biomass, population levels, foraging rates, etc. are still needed in order to calculate rates of movement for nutrients and energy. This is particularly true of groups which influence the rate of accumulation of nutrients in the system or higher taxa which may regulate ecosystem structure (Glasser 1979).

The movement of energy and nutrients from producers to consumers was not considered quantitatively during Phase I. Herbivory studies are planned for Phase II which will take into account aspects of trophic organization which were identified in the first phase. Vertical stratification, seasonality, and the existence of day and night food subwebs will be considered in the development of the sampling program. Preliminary studies indicate that a substantial amount of total herbivory is performed by sucking insects (e.g. planthoppers and leaf-hoppers); therefore leaf area indices which estimate grazing will be supplemented with appropriate methods to determine the importance of sucking insects.

Soil and litter fauna received little attention during Phase I because of manpower limitations and logistic constraints but we believe them to be important in terms of overall decomposition processes and overall animal biomass. Obtaining qualitative and quantitative information on these groups will be a primary objective of baseline data collection during the second phase of our cycling and transport program.

Additional chemical analyses are planned in conjunction with other sampling studies in order to determine rates and patterns of movement for selected elements. Nutrient export will be investigated by establishing a stream gage and analyzing the chemical content of samples taken during periods of normal low flow and during rain fall events. These studies will provide essential data for addressing questions concerning critical nutrients in tropical rain forest ecosystems (Jordan and Herrera 1981).

Experimental manipulations will also be undertaken during the second phase of this program. Habitat modification within the study site will be of a limited nature and will be approved in advance by

Table 44. Common (=mostly likely be seen) invertebrates of the vicinity of the El Verde Field Station. Taxa are identified to genus or species except for most holometabolous insects.

- Class: Mollusca
  - Order: Stylommatophora
    - Family: Camaenidae
      - *Caracolus caracolla*
- Class: Arachnida
  - Order: Acarina
    - Family: Oribatidae
    - other families
  - Order: Araneida
    - Family: Theraphosidae
      - *Cyrtophilos portoricae*
    - Family: Uloboridae
      - *Miagrammopes ciliatus*
    - Family: Pholcidae
      - *Micromerys dalei*
      - *Modismus sexoculatus*
    - Family: Ctenidae
      - *Oligoctenus ottleyi*
    - Family: Sparassidae
      - *Olius* spp.
    - Family: Salticidae
      - several spp.
    - Family: Araneidae
      - *Leucage regnyi*
  - Order: Amblypygi
    - Family: Phrynidae
      - *Phrynus palmatus*
  - Order: Pseudoscorpionida
    - Family: Menthidae
      - *Menthus* sp.
- Class: Chilopoda
  - Order: Scolopendromorpha
    - Family: Scolopendridae
      - *Scolopendra alternans*
- Class: Crustacea
  - Order: Isopoda
    - Family: Oniscidae
      - *Philocia richmondi*
  - Order: Decapoda
    - Family: Potamonidae
      - *Epilobocera situatifrons*
- Class: Collembola
  - Order: Collembola
    - Family: Entomobryidae
      - *Dicranocentropha* spp.
      - *Dicranocentruga* spp.
      - *Lepidocyrtus* spp.

- Class: Insecta
    - Order: Blattodea
        - Family: Blattellidae
            - *Cariblatta* spp.
            - *Epilampra wheeleri*
            - *Plectoptera* spp.
    - Order: Orthoptera
        - Family: Tettigoniidae
            - *Anaulocomera laticauda*
            - *Microcentrum triangulatum*
            - *Turpilla rugosa*
        - Family: Gryllidae
            - *Amphicausta caraibea*
            - *Anaphixa* sp.
            - *Anurogryllus muticus*
            - *Cyrtoxipha gundlachi*
            - *Gryllus assimilus*
            - *Orocharis* spp.
    - Order: Phasmodea
        - Family: Phasmatidae
            - *Lamponius* sp.
    - Order: Isoptera
        - Family: Termitidae
            - *Nasutitermes costalis*
    - Order: Psocoptera
        - serval families
    - Order: Homoptera
        - Family: Cicadidae
            - *Borencona aguadilla*
        - Family: Cicadellidae
            - *Sibovea coffeacola*
            - *Xestocephalus maculatus*
        - Family: Cixiidae
            - *Bothriocera undata*
            - *Pintalia* spp.
        - Family: Delphacidae
            - *Ugyops occidentalis*
        - Family: Derbidae
            - *Dawnaria sordidulum*
        - Family: Tropiduchidae
            - *Ladella stali*
        - Family: Flatidae
            - *Petrusa* spp.
        - Family: Issidae
            - *Colpoptera* spp.
    - Order: Coleoptera
        - Family: Staphylinidae
        - Family: Pselaphidae
        - Family: Ptiliidae
        - Family: Lampyridae
            - *Photinus* spp.

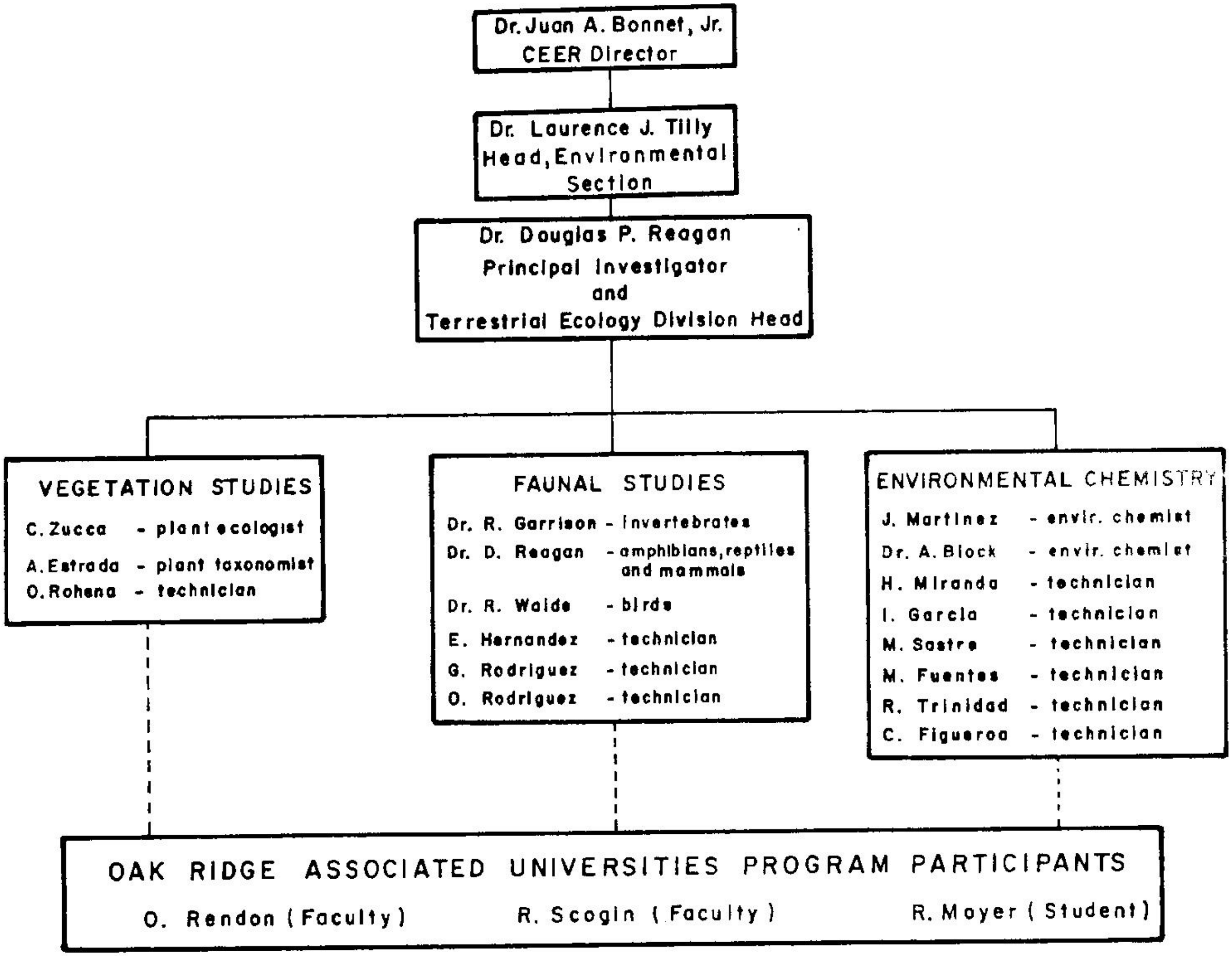
Family: Scolytidae
    subfamily Ipinae
Order: Lepidoptera
  Family: Pieridae
    Dismorphia spio
  Family: Noctuidae
    several spp.
  "Microlepidoptera"
    several spp.
Order: Diptera
  Family: Tipulidae
  Family: Psychodidae
  Family: Culicidae
  Family: Ceratopogonidae
  Family: Chironomidae
  Family: Mycetophilidae
  Family: Sciaridae
  Family: Cecidomyiidae
  Family: Stratiomyidae
  Family: Dolichopodidae
  Family: Phoridae
  Family: Drosophilidae
  Family: Anthomyiidae
  Family: Tachinidae
Order: Hymenoptera
  superfaimily Chalcidoidea
  Family: Scelionidae
  Family: Formicidae
    Iridomyrmex melleus
    Myrmelachista ramulorum
    Pheidole moerens
  Family: Vespidae
    Myschcocyttarus cubensis
  Family: Apidae
    Apis mellifera

the Institute of Tropical Forestry of the U.S. Forest Service which has jurisdiction over the land. Larger scale disturbances will be investigated in conjunction with planned U.S. Forest Service manipulations at nearby locations within the same forest type. Research will also be conducted in areas of forest with a known history of disturbance (e.g. plantations, land slides, successional areas). These should provide relevant information on the nutrient content, biomass, food web structure, etc., which will enable us to evaluate the impacts of different types of disturbances of natural rain forests, and will allow us to evaluate long term aspects of disturbances without having to wait for several years before sampling.

The overall program for this next phase of research will expand upon Phase I by continuing to gather baseline information on mature natural forest. Phase II studies will be more quantitative and will focus on key pathways and major food chains. Experimental manipulations are an important aspect of the Phase II effort and will emphasize the evaluation of impacts which may result from implementation of various energy development alternatives on natural tropical rain forests.

7.0 PERSONNEL AND ORGANIZATION

Figure 27. Project Personnel for the Rain Forest Cycling and Transport Program



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9.0 APPENDIX I

SPECIES:
PLACE:
DATE:
[illegible]

TIME:
WEATHER:
OBSERVER:

OTHER:

	L	R	3	6	9	12	15	30	60	120	sing	height
Ruddy-Quail Dove												
Bananaquit												
Puerto Rican Tody												
Red-necked Pigeon												
Pearly-eyed Thrasher												
Lizard Cuckoo												
Puerto Rican Woodpecker												
Red-legged Thrush												
Black-whiskered Vireo												
Stripe-headed Tanager												
Puerto Rican Tanager												
Puerto Rican Bullfinch												
Red-tailed Hawk												
Puerto Rican Emerald												
Elfin-woods Warbler												

F I E L D   R E P O R T I N G   F O R M

Permit no.		Station		Bander		Recorder	
Species AOU no.		Scientific name		Common name			

Capture Number	Band Color	Hour	Height	Net Mesh	Age	Sex	Weight	Color of:				Skull Oss.	Wing Chord	Tail	Tarsus	Culmen	Bill Depth	Bill Width	Molt	Notes
								Eye	Leg	Foot	Mouth									

SPECIES: SEX: OBSERVER: PLACE:

DATE	TIME	COM/ACT	TREE	HEIGHT			BEH	DIR/DIST	SUB	ITEM	PEREL	CROW	COMMENTS
				C	T	B							

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E. Huertas-Correa conducted the minimum area curve study, Ana J. Correa, Rosa M. Tomassini and Eva Cortês typed the manuscript and Pedro J. Sotelo did the art work.