CEER-T-197 TROPICAL RAIN FOREST CYCLING AND TRANSPORT PROGRAM PHASE 1 REPORT

Prepared by: Douglas P. Reagan, Rosser W. Garrison, José E. Martinez, Robert B. Waide, Carol P. Zucca

TERRESTRIAL ECOLOGY DIVISION
CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO
SAN JUAN, PUERTO RICO
JUNE 1982

TROPICAL RAIN FOREST CYCLING AND TRANSPORT PROGRAM PHASE 1 REPORT

Prepared by: Douglas P. Reagan, Rosser W. Garrison, José E. Martinez, Robert B. Waide, Carol P. Zucca

TERRESTRIAL ECOLOGY DIVISION
CENTER FOR ENERGY AND ENVIRONMENT RESEARCH
UNIVERSITY OF PUERTO RICO
SAN JUAN, PUERTO RICO
JUNE 1982

1.0 SYNOPSIS
2.0 INTRODUCTION
3.0 PROGRAM OVERVIEW
4.0 PHASE 1 METHODS
5.0 RESULTS AND DISCUSSION

TABLE OF CONTENTS

5.1 Sampling Design
5.2 Task Methods
5.3 Physical Phenomena
5.4 Elemental Inventory and Energy Studies
5.5 Vegetation Studies
5.6 Plot Characterization
5.7 Phenology
5.8 Litter Fall
5.9 Loose Litter
5.10 Decomposition
5.11 Faunal Studies
5.12 Invertebrates
5.13 Amphibians and Reptiles
5.14 Birds
5.15 Mammals

Continued Table of Contents

6.0 INTEGRATION
6.1 Ecosystem Organization
6.2 Phase II Research
8.0 PERSONNEL AND ORGANIZATION
9.0 LITERATURE CITED
10.0 APPENDIX I
11.0 ACKNOWLEDGEMENTS

LIST OF TABLES

1. Decomposition values (per cent original dry weight; standard error in parenthesis)
2. Sample sizes of Anolis lizards used in

Evaluating food data: Elemental composition and caloric value of amphibians, reptiles, and bats. Also, the inorganic ion composition of amphibians, reptiles, and bats. Elemental composition and caloric value of bird tissues. Inorganic ion composition of birds and their feathers.

Population densities and weights of amphibians, reptiles, and bats. Coens Elemental standing crops of amphibians and reptiles. Basal area (B.8.), density (Ind /ha), and importance values (I.V.) of the ten most significant species of trees among four plots.

List of species in each family, including average basal area (BA m2/ha) and density (Ind/ha) for each family. Species symbols and corresponding scientific names for trees at ET Verde.

Mean monthly litter fall values (g/m2) by categories for 1981. Mean monthly leaf fall of four plots in g/m2 for 5 years, including the 5-year mean. Yearly totals and rates in g/m2 per day are also given. One-way analysis of variance among litter fall and leaf fall in 1981. F values demonstrate significance among plots, months, and years.

Comparison of cycling and storage components by latitude. Components of litter fall (in percent) expressed as means of four plots in 1981. The standard error is in parenthesis. Rainfall in mm from ET Verde during the litter fall study period.

Page 22, 39, 40, 45, 31, 82, 96, 58, 59, 82, 6

Table 12, 19, 20, 21, 22, 23, 24, 26, 27, 28, 29. Mean leaf fall input (g/m2 per year) by species, demonstrating between plot variability and mean contribution to total forest. Plot A refers to the 1973 collection, while plots 1-4 demonstrate input during 1981.

1981 mean leaf fall (g/m2) values from four plots for 10 species of trees. Plot and seasonal comparisons of mean loose litter values in g/m2. The value in parenthesis represents the standard error. F values from one-way analyses of variance of loose litter among plots at each season. F

values from one-way analyses.

Analyses of variance for loose litter between wet and dry seasons. Leaf fall and miscellaneous loose litter (kg/ha) and turnover rates (TOR = leaf fall/misc. loose litter) by plot and season.

Species composition and g fresh weight/species in decomposition position. Numbers of invertebrates collected over 10 days, 8 nights, 9-22 June 1981. Numbers of invertebrates collected (by order) for day, night, combined totals, and percentage composition of overall total. Day-night totals are from 10 day and 8 night samples.

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 6 are 4 and 3 bags respectively wet seasons.

Prey taxa consumed by four species of Anolis in dry and wet seasons. Stomach contents for four species of Anolis lizards during dry and wet seasons. N= number of lizards per group. Stomach contents for four species of Anolis lizards during dry and wet seasons. N = number of lizards per group. All volume estimates are on page % a 7 n 78 9 81 82 86 92 99 108 m.

Table Page 3. 32. 3. 3a. 35. 36. 37. 38. 33.

Vertebrates recorded from the El Verde Study Area. Anurans observed along transects during 1980 wet season surveys. Relative abundances of the three common anoline lizard species during wet and dry season surveys at four randomly selected locations within the study area.

123 Mark and resight data for dry season 1981 tower surveys. Population density estimates obtained by three standard methods for Anolis stratulus at the tower during the 1981 dry season (February-March). Number of captures and capture rates for various bird species for plots 1-4.

Population estimates by territory mapping and Time transect methods. Territory maps were made between 2 June and 13 July 1981 and transect.

Counts were taken between 22-29 June 1981. The number of territories is multiplied by 2 for females and divided by the area sampled to get density. Transect densities are calculated following Elen (1971)....... 141

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) M2 149

Preliminary data on the diet of 14 bird species are provided. The number of birds color-banded and the number of stomach samples obtained are listed in Phase Two.

Means and their standard error for bill length and bill width of birds caught in Phase I are presented. Birds in immature plumage and females are lumped in (8) » 182

Means and their standard error for bill length and bill width of birds caught in Phase I are presented again. Birds in immature plumage and females are lumped in (9).

Key species and species groups in the trophic structure of the El Verde rainforest are identified in Phase One. Common invertebrates of the vicinity of the El Verde field station are also listed. Taxa are identified to genus or species except for most holometabolous insects... 162

LIST OF FIGURES

Figure, n. a 13. 4 15, 16 Ww, Generalized Ecosystem Model. Cycling and Transport Program study area. Sampling design for minimal area study. Vegetation sampling locations within study plots. Minimal area curve for El Verde (102). Minimal area curve for El Verde (52). Five-year mean leaf fall plus or minus one standard. Components of litter fall (means of four plots). Loose litter components by plot and season. SS-STP for differences in mean numbers of insects among various height intervals. SS-STP for differences in mean numbers of Fulgoroids per 6-meter increments (1st meter deleted). Mean prey size for Anolis at El Verde. For each variable, the midpoint equals the mean, the horizontal line equals the range, the black portion equals 96 standard errors, and one half of each black bar plus the white bar at either end equals one standard deviation. The percentage of invertebrate larvae consumed by birds is also provided.

Anolis species are invertebrate scavengers, herbivores, and predators. The vertical distribution of adult Anolis stratulus was observed more than ten times at the tower from February-April 1981. The vertical distribution of subadult Anolis stratulus was observed more than ten times at the tower from February-April 1981. The vertical distribution of Anolis species during the wet season, September-November, was recorded.

Figures 18 through 26 show the vertical distribution of Anolis species during the dry season (January-March 1987). Seasonal changes in population densities were tracked from transect counts at El Verde. These counts recorded seasonal changes in abundance for several bird species including Red-necked Pigeons, Puerto Rican Todies, Black-whiskered Vireos, and Bananaquits in four different plots at El Verde.

The foraging heights of 10 common bird species at El Verde were also documented.

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. This will help us adequately evaluate the ecological consequences of energy development. The original program plan was established in June 1980. Despite modifications, the basic approach has not been altered. A primary objective of Phase 1 was to identify major reservoirs.

Nutrients and energy within the forest 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 a tabonuco forest within an elevational range of 250-300 m. The 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 200 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 1961 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 1 with four years of similar investigations (1970-73) in the same area. No annual differences were detected among the four sample plots in Phase 1, 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 the beginning of the wet season (March-June). A value of 1.389/m^2 day was obtained from the combined five years of data. These results are similar to the estimate of 1.439/m^2 day.

The research conducted by Wiegert in 1965-66 in the same area was obtained for the irradiated rain forest program in 1970. This consistency in the 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 this 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 a 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. Therefore, our field efforts 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 the red-necked pigeon. The Puerto Rican boa is larger (2-3 kg), but it is rare within the study area, and probably uncommon throughout the forest (Reagan and Zucca 1962).

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 due to 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 make them more important in the food web.

The food web at El Verde compared to mainland sites where these groups are less common is distinct. Analyses elucidated the pathways of movement between compartments within the food web. Feeding observations and gut content revealed the presence of vertical stratification of foraging among major taxa, feedback loops with large invertebrates, (e.g. tailless whip scorpions, 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 suctorial mouth parts. This indicates that previous studies 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 decomposition, 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 decomposition of leaves seem to function consistently.

The text has 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 once 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 formatted prior to funding changes for the 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 and summarizes important findings from separate tasks. 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 is profound. 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.
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 patterns 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 further research.

Simulation of cycling and transport processes, area & generation of hypotheses concerning the potential impacts of tertiary development which are both relevant to tropical forest ecosystems and testable in Phase 1. The elemental and caloric inventory provides 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 1 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) 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 (excluding 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. More focus was 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 consumer 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 El Verde.

Station. Other factors evaluated in the study area delineation process included 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 1878). Sampling points were selected using a grid technique (Phillipe 1989). 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 40 feet of a sampling point.

Figure 1. RESPIRATION [courses with decomposers—excretions and corpses]. TERTIARY CONSUMERS - SECONDARY CONSUMERS - CONSUMERS - PRODUCERS (PLANTS). Generalized Ecosystem Model.

Figure 2. Study Area Boundary - Nine Vector Grid - Permanent Stream. Cycling and Transport Program study area.

Sample points were no closer than 200m to each other to avoid sampling overlap, 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 plot with boundaries marked at 10m 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

The task and subtask are described as separate entities within the overall Phase I sampling design due to the variation in pertinent information already available for different disciplines. The tasks had 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:
(Page Break)
To collect pertinent weather data to be used in evaluating information collected from other tasks to document seasonal and other temporal changes within the study area. Materials include rain gauges (at 1 Verde Station and the tower), thermometers, and hygrothermographs (at 1 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 homogeneous 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 non-volatile matter, the crucibles were placed in a hot water bath and the residues were allowed to dissolve in 50% HCL for one hour. 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 acidic conditions. Color intensity becomes stable within one half hour and is measured at 470 nm. Light absorbance determinations were performed in a Zeiss PH-2 U-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 diffused 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 2 Model 1108 oxygen bombs. 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. Vegetation Studies Analysis of the vegetation was designed to determine the variation.

The ability within the Tabonuco forest type was measured by important storages and flows. These baseline data are intended to be used in the planning of Phase II experimental research.

4.2.3.1 Plot Characterization

Certain types of information were needed to provide a basis for interpreting floral and faunal data and for designing future investigations. The techniques used were as follows:

Subtask 1: Minimal Area

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 randomly selected 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 with 5 cm diameter were identified and included in the study. The minimal area, as defined above, was determined.

Subtask 2: Structural Analysis

Objective: To determine the standing crop for each species.

Plot 3 (Figure 2) was selected as the best representation of the four forest plots and thus was the most thoroughly studied. PVC tubing was used to establish an 8 10x10 m grid in a 1 ha area (plot 3). All vegetation with a diameter of 10 cm or more was identified, mapped, measured, and tagged. A sub-sample of this plot was selected to be analyzed as above within a 5 m radius of each of twenty randomly located litter baskets. Comparisons were then made between the total plot analysis (10,000 x2) and the sub-sample (1570 m²). Plots 1, 2, and 4 were structurally analyzed as in plot 3 using the sub-sample technique. Basal areas (m²/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 the importance of the contribution of each species to flower and fruit fall among plots.

Comparisons of flowering and fruiting patterns were measured using materials collected in the litterfall baskets (refer to section 4.2.3.3 for litter sampling information).

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 elemental content analysis.

4.2.3.3 Litter Fall Objectives: To determine the 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 ET Verde.

Twenty 1m² galvanized hardware cloth baskets lined with 1mm mesh fiberglass screen were placed in each of the four plots. Locations of the four litterfall transects were randomly selected at each site with 10m intervals between potential transect lines. Five baskets were randomly placed along each transect (Figure 4). Each basket was placed at least 10cm from the forest floor (30cm 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 hours, 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 m²) were collected at random in each plot each season. Forty samples (two at each litter basket) were collected.

Figure 4. Vegetation sampling locations within study plots.

The following text has been corrected for spelling, grammar, and punctuation:

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 smaller than expected sample variability in the dry season as well as 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 areas 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 macro-decomposers, 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... (Page break)

The ground near each of 26 randomly located Vitter baskets contained 80 bags in total. In addition, 40 bags were placed in a topographically homogeneous area (known as plot X). Ten bags were reserved for the measure of zero-time wet weight to dry weight. 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 established to 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 the percentage 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 32 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 were 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. In the 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 valuable insights.

Table 1 depicts decomposition values per cent of original dry weight, with standard error in parenthesis. The samples are listed in a seemingly random order, such as 2, 14, 7, 100, 14/3, and so on.

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

x: Leaves from plot 3; placed in topographically homogeneous plot x

May 1981

3: Leaves from plot 3; placed randomly in plot 3

3a: Leaves from plot 3; placed in plot 4

4: Leaves from plot 4; placed randomly in plot 4

x: Leaves from plot 43; placed in plot x

October 1981

3: Leaves from plot 3; placed randomly in plot 3

4: Leaves from plot 4; placed in plot x

Page Break

Valuable information on the roles of animal populations as nutrient "sinks" and as agents of nutrient transport (Hair 1966, Stokes 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. Due to the large number of different intermediate consumers, their roles and rates will need to be estimated collectively. This estimation will be derived from the differences between the 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. Due to 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) play an important part in the Luquillo Forest ecosystem. A major challenge has been the proper identification of the multitude 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 (Orewry, 1970), but the true number is probably greater than 3000. Many authors (e.g. Janzen and Schoener, 1966; 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.

Puerto Rican Arthropods: Some groups, such as the Auchenorrhynchus Homoptera, are fairly well-known due to their common and conspicuous presence. However, other groups, such as mites and certain Diptera, are less understood due to time and budget limitations. Consequently, we have been forced to categorize these invertebrates at higher levels, such as families and orders. A reasonably complete overview of the important groups of invertebrates inhabiting the Luquillo Rain Forest is not currently available, and less is known about their seasonal abundance and population turnover rates. Nevertheless, 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 provided valuable insights into the role played by many macroarthropods in the food web. These findings also support various samplings of the invertebrate fauna we have conducted at different times throughout the year.

Page Break

In addition to the curated research collection at the El Verde Field Station, the following taxonomic references were helpful in identifying invertebrates: For invertebrates in general - Brues et al. 1954, Hickman 1973; spiders - Kaston 1978, Petrunkevitch 1929, 1930, Velez 1971; sowbugs - Velez 1966; millipedes - Velez 1966; 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 1950, 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.

During the rainy season, the aim was to determine significant differences, if any, between 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 1961. After the identification of invertebrates was completed, results were tabulated and mean numbers were compared using 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 macro decomposers of leaf litter. Determine possible changes in species make-up over time, and 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 2x 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 Jax 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% ethanol and identified to the 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 bags 4 and 4 which contained four and three bags respectively.

Subtask 3: Anolis Food Habits
Objectives: Determine if different species (Anolis cuvieri, A. undulachi, A. evermanni, A. stratulus) show preferences for certain invertebrate preys. Determine diet overlap, if any.

The text should be corrected as follows:

"Determine if Anolis species 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 various 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, which 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 Rio Sonadora and surrounding area so that they could be compared with forest specimens. The entire contents of each stomach was examined, and identities to the lowest taxonomic category (to species, if possible) and length were determined.

Table 2. Sample sizes of Anolis lizards used in evaluating food data vary seasonally. A. cuvieri: 7, A. gundlach: 10, A. evermanni: 13, A. stratulus: 4. Data includes 10 specimens from the edge of Rio Sonadora, a rainforest habitat.

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

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 relative abundance of amphibian (anuran) species within the study area in order to identify important species and to 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. 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

Objective: To obtain minimum and relative population density estimates for common species of Anolis at four randomly selected locations within the study area. To estimate the absolute density.

The canopy species, Anolis stratulus, was studied at the tower within the study area. Minimum and relative population densities were determined through a permanent transect 180 m long that was established in each plot. This transect extended 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 both wet and dry seasons. The species, sex (or size class), and distance to the centerline were recorded for each observed lizard. Relative abundances were computed and minimum population densities were calculated according to Frye's strip census technique (Overton 1971).

Population density estimates for Anolis stratulus 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 rainforest.

Casual observations from the 22m tower in the forest 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 using the following procedures:

Fifteen transects were conducted at each of three times of day: morning (0700-1000), midday (1000-1430), and afternoon (1430-1830) for a total of 45 transects during the wet season of 1960 (September - November), and again during the dry season of 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 22m transect for each species.

Data were analyzed by species, season, and time of day 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 the 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 1 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 Hernandez 1962). 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 the counts.

After the termination of one year of monthly counts, subsequent sampling was conducted at two-month intervals (August and October 1961). Afternoon counts beginning at 1800 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 120m from the transect line or more than 30m 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.

Sight, song, and call were recorded separately. A sample data sheet is presented in Appendix 1. Population densities were individually calculated for each detection class following Enlen (1971). Results are reported individually 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. (1960).

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 1. 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 Fasborg 1973, MacArthur and MacArthur 1974).

Spot maps - A grid with lines at 4 m intervals was established in a 29 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 birds were 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). The 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 hectares of the study site.

Subtask 2: Feeding Behavior

Certain parameters were set for observing the feeding behaviors of the birds. 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 1. Foraging data collected in the Luquillo National Forest by Carmen Fon 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, species, 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 tartrate (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 202 ETOH. Birds captured during marking studies had 0.1 ml of antimony potassium tartrate solution introduced into their stomachs via a syringe and tygon tubing. Each bird was placed in a closed container for 15 minutes, 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 site 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 per individual of each species per unit time. Although completion of this subtask has been postponed until Phase 2, the methods to

The text should be corrected as follows:

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 be 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 per individual per unit time will be calculated.

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 root 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.

The text, once corrected, reads as follows:

And on the Rio Sonadora footbridge 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 were obtained from gut analysis of a single Stenoderma Rufum captured at a low net in July 1961. 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 were recorded, and each was marked with 2 different paint markings 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, interpretive 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 rainforest during the mid-1960s. The tower station was established in July 1960 and will be maintained throughout the program field studies. Prior to the implementation of Phase...

II studies a rain event. A full event recorder will be installed at the tower, and a wind (velocity and direction) gauge and a stream flow gauge 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 sulfur. 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.

[The following text is unclear and may require more context or original source for accurate translation.]

Inorganic composition of amphibians, reptiles, and bats. Table 4. Sex lactylus Eleutherod evermannt A. gundlachi ‘cogu Anolis -40- + .56 17.62 + 2.30 18.344 5.15 $3.03 5.17 + 2.09 5.55 + 2.03 4.80 + £04 a5 4.15 1.86 + 44.36 + 2.48 42.55 + 3.08 72 W F ma/9 dry weight. of ary weight. expressed in % of difference bet from their average. z + indicate difference Ino Ash

[The following text is unclear and may require more context or original source for accurate translation.]

I'm very sorry, but the text provided is too scrambled and unclear for me to be able to offer a meaningful correction. If you could provide more context or a clearer version of the text, I would be glad to assist you further.

to 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 0.163 of their dry weight. Sulphur values varied between 0.6 and 15, but the average of all species combined was approximately 0.75 percent. (Frogs were an exception as they averaged only 0.262). 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 fibrils.

2. Calorimetry

The caloric value of all materials analyzed remained around 5,000 J/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, unpublished 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), Grow (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

The physical environment, including water and energy regimes, has effects on soils and topography (Brunig and KIinge 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 comparisons among other natural forests and plantations. The present studies were designed, therefore, to measure and compare.

The 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, based on the design of Mueller-Dombois and Ellenberg (1974), indicated that a plot size of 2180 m^2 would yield a 10 percent increase in the number of new plant species (Figure 5). A plot area of 3400 m^2 would yield a 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 2970). One ha would also assure valid results with multiple plot usage.

The tabonuco forest basal area of live trees with a diameter at breast height (DBH) of 10cm or more averaged 30.75 m^2/ha across the four study sites. This value is within the range (17-50 m^2/ha) reported by Sortano-Ressy et al. (1970) and Odum (1970), and close to the 35.7 m^2/ha value that Crow (1980) reported for studies in this area.

A nearby 60-year.

The old multi-species natural succession stand had a basal area of 27.9 m^2/ha; a 40-year-old plantation of Calophylium calaba had 30.2 m^2/ha; and a 17-year-old plantation of Pinus caribaea had 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. Judging by species composition and canopy cover, plot 4 is disturbed. The basal area of plot 4 (24.8 m^2/ha) supports this premise. Plots 1 and 3 with basal areas of 39.0 and 34.3 m^2/ha respectively, fall within the range represented in Puerto Rico as a mature forest. The mean density of the study site trees was 729 ind/ha. Wadsworth (1981) reported 655 ind/ha in his measurement of a virgin tabonuco forest near El Verde. The densities of plots 1-4 (Table 9), were 247, 738, 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 species.

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 values Cottam and Curtis 1956). Two species, Dacryodes excelsa (tabonuco) and Prestoea montana (sierra palm) were dominant in all four plots: five (Bc, Wor, Ifa, Ok and Sb; see Table II for species symbol key) in three plots; two (Cp and Cep) in two plots; and thirteen (Ap, Ce, Da, Dm, Gt, MD, Mg, Mys, NS, Ol, SI, Thy 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 area (BA m^2/ha) and density (Ind/ha) for each family.

Family	Species	BA m^2/ha	Ind/ha
Leguminosae	Ai, Ifa, Iv, Ok	43	54
Palmae	Prm	3.8	197
Euphorbiaceae	Aly, APs, Cb, Dg, Sl	3.7	7
Burseraceae	De, To	3.5	6
Flacourtiaceae	Ca, Cbi, Cs, Hor	3.2	75
Elaeocerpaceae	ey	2.2	45
Combretaceae	Bc	18	10
Meliaceae	be	15	8
Sapotaceae	Mo, Mg, Mic	13	7
Lauraceae	Bp, Ns, Ol, Om	1.2	8
Moraceae	Cep	12	10
Araliaceae	Da, Dn	1.0	18
Bignoniaceae	Th	0.6	10
Melastomataceae	Sg, Mt	0.4	16
Myrtaceae	Es, Yd, Mys	0.4	16
Rutaceae	In	0.3	3
Annonaceae	Oka, OT	0.1	8
Boraginaceae	Csi	0.1	6
Oleaceae	Id	0.1	3
Sapindaceae	Ma	0.1	2
Nyctaginaceae	Pia	0.08	2
Polygonaceae	Cos	0.02	2
Rubiaceae	a	0.02	2

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

Species Symbol	Scientific Name
a	Andira inermis

a | Alchornea

Despite species composition differences, the tabonuco forest type consistently cycles the same amount (g/m) of leaves annually from trees to the 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/m² for 5 years including the 5-year mean. Yearly totals and rates in g/m²/day are also given.

Year	Month	1970	1971	1972	1973	1980	5 yr. mean
January	21.1	26.7	30.3	20.5	26.5		
February	22.7	29.8	28.8	-	28.3		
March	43.7	2.9	36.2	57.5	48.9		
April	47	74	99.3	86.5	-		
May	67.5	48.9	57.7	-	42.5		
June	57.6	59.6	55.2	-	58.0		
July	45.0	-	-	-	-		

45.1, 46.7, 3158.7, we, A, 5, 407, 5.8, we, 66, ae, s, 4.6, 542, 32.8, 64.1, a7.9, 42.5, 8.7, 4.1, 30.6, 301, ae, 30.4, 4, 5.8, 185, 27.525, 24.8, o, 0, 283, 6, sans, 24.7, Neat, se, 309, a0, eto. ane, 505.9, g/t, ay, 1.46, 1.45, 1.27, 1.40, 1.35, 1.39, ee.

Table 14. One-way analysis of variance among Titter fat and Teat fal in 1981. F values demonstrate significance among plots, decays, and years. See Litter, fant Leaf fall ‘among ns ns plots 0.10! 0.18' ‘mong 12 ae ee mos. 19.3) 14.8) ‘Among 5 ns years, not available 0.22 oo ms = p> .05 =p < L001.

15. Comparison of cycling and storage components by Ttttuse, 5, 3, i, i, i, She, SM, re, i, Mat, ogee, es, se, mee. vn, ect, ey, HTT, "rain, Grub, 197, i, eg, Bree, sa, az, a, ah, 1979, ein? H, we, SAF, Si, feet, EE, 1.9, 0.7, Bray and Gorham, 1964, -67.

(cut) 802 (ort) or ee eu uo (22) 8°02 (a°¢) 9°64 ws (62) ees a (re) (9'1) ovet oe (0) 0+ N ( ) 96 ors 0 (29) ¥°82 (s'2) 62 (0) V2 s (ere) eee (eee (yee (oz) say v (we) (c0) 82 (oz) € —(6°2) L09 e (v2) 162 (s°0) et 0) St (8'1) 9°96 e (sy) get (f°0) 9°0 (e0) 80 (S"%) s*s9 " « (yo) so (ee) L958 ¥ (ez) eo (c-0) rt (v0) 60 (9"t) €*99 W €) 6°52 {e°L) ov (90) Ut ois 4 (o') 9a (ce) eon (20) st ores snoaue| {39ShH oom, aang aeMOLy ‘sane37 yaUOH “sisayquaued uy s1 so4sa paepuers HL “GGL Us $2010 unos 40 sueaw se passaidxa (quaa ued us) {Les 49935 40 sauaveduey “91 aiqey 68+

B, vee, 1, Fievers, ene, Fratt, GD, wiscrne, ue, Montne, four plots. Components of litter fall (means of Figure 8. 69.

Rainfall data are summarized in Table 17. A Tones regression comparing litter fall to rainfall showed little correlation (R^2 = 1.16). 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 19/3 (Estrada, unpublished data). Although leaf fall input.

The text 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-year-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 the 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 -70.

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

Year Mean Mean Months

1970 (Jan) 646.5 (Feb) 308.3 (Mar) 256.3 (Apr) 216.6 (May) 208.4 (Jun) 249.5 (Jul) 109.2 (Aug) 277.1 (Sep) 233.1 (Oct) 200.2 (Nov) 193.8 (Dec) 78.7

Yearly total (mm): 3923.4, 2612.9, 2188.5, 3672.1, 3148.0, 3602.5.

Please note that certain data seem to be missing or incomplete in the original text.

(In) 154.5, 102.0 are 152, 123.9, 137.9.

Table 18 illustrates the mean leaf fall input (a/n" year) by species, indicating between plot variability and mean contribution to total. Forest lot A refers to the 1973 collection while plots 1-4 consecrate input during 1981.

Mean total of species per plot (g/m² per year):

Species	Plot A	Plot 1	Plot 2	Plot 3	Plot 4
De	69.9	107.9	78.0	N/A	22
Be	7916	35.3	350	63.1	46.7
Ca	753.3	N/A	6136	N/A	N/A
Ag	99	102.4	26.9	5	N/A
Ifa	10.0	83	64.1	10.3	20.3
Ok	22.6	5	25.8	23.0	38.4
Cy	4.8	41	9.2	4	0
Ot	N/A	0.0	0.4	6.0	66.3
Cep	778.4	0.7	1.9	28.7	20.2
Hor	3.3	16.6	3	5.2	14.2
Sb	29.2	30.7	N/A	18.9	3
Rg	64	36.8	9.8	N/A	N/A
Pr	188	3	N/A	21.9	6
Cr	0.0	20.5	148	3	68.3
Ma	N/A	0.0	0.0	0.0	55.6
Cp	5.5	2.0	N/A	N/A	13.2
81 other species	45.0	0.0	48	N/A	126
Total	502.5	451.4	491.9	509.3	512.8

At increasing latitudes, Jenny et al. (1989) state that in a Colombian forest, loose litter (1076 g/m²) was one-tenth the loose litter in a Californian forest (11609 g/m²), while litter fall in the Colombian site (1023 g/m²) was five times the value from the Californian site (200 g/m²). Table 15 gives comparative latitudinal litter storage values. Selmy et al. (1949) calculated from litter fall rates and storage values that it would take a Colombian rainforest 1-3 years to reach equilibrium; in California, it would take 26-332 years depending on the forest type (oak or pine) and altitude. Ground litter storage in the four study plots in El Verde is 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/m². This value is considerably lower than Ketgert's (1980) El Verde mean of 598 g/m^2.

Continued analysis is needed for the four plot, two-year study.

The mean season 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. The 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 a 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.

Wet Season Loose litter components by plot and season Figure 9.

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

Wood Miscellaneous Total

Dry Season 2.41 1.59 2.00

Wet Season 3.16

7,794 2.478 6.2 3.76 ns = p> .05 se = 9 < .001 -7-

Table 22: Wood Plot

Plot 1: 5.01
Plot 2: 11.97
Plot 3: 0.208
Plot 4: 1.43

Combined plot comparison: 9.7406

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

Miscellaneous Total: 26 58 2.5608 7.50 1.58 0.03"* 0.02" 158. 3.876 3.998 1.58 3.35" 8.6 1.238

Table 23: Leaf 211 and miscellaneous loose litter (kg/ha) and turnover rates (TOR = leaf fall/misc. loose litter) by plot and season.

Dry Season:
Leaf fall: 4514 491950935128
Miscellaneous: 295625602038
Loose litter TOR: 830 92 72

Wet Season:
Leaf fall: 217 gsl 4195093129
Miscellaneous: 2784 20723000
Loose litter TOR: 2.3770 2051.90

Yearly Mean:
Leaf fall: 4195093528
Miscellaneous: 287023162563
Loose litter TOR: 87 202

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 usable 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 (Neigert 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 did not show significant differences in the time of field placement up to 120 days. However, 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 year. Thus, factors other than decomposition must account for the rapid TOT; some organic matter may be incorporated into soil organic matter or lost.

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

Species	Weight (g)
Species 1	0.7
Species 2	0.6
Species 3	0.8
Species 4	0.5
Species 5	0.3
Misc.	1.8
Total	10.0

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

Day, Night	ARTHROPODA	Arachnida	Insecta
1	Acarina Oribatidae	Araneiaa unidentifiable to family	Epheneroptera Leptophiebtidae
2	Photcidae unidentifiable to family	Modismus sexoculstus	Blattodea Blattidae Blattellidae
3	Araneiéae unidentifiable to species	Leucage regnys	Orthoptera Ory at Grocheris vaginalis

Terebrans Cyrtoxiphe “Gundtachi” Undetermined Trigonidinge Isoptera Kalotermi Tidae Glyptotermes Pubescens (winged) 3 2 Termitidae Nasutitermes sp. Psocoptera Lepidopsocidae v2 Polypsocidae Epipsocidae Psocidae “82.

Continued table 25 Tysanoptera Phlacothripidae 8 10 Thripidae 5 2 Hemiptera Dipsocoridae 1 Niridae undetermined species 1 Polymerus Pallidus 1 Lygeetdse 6 Cydnidae 1 Homoptera Menbracidae Nessorchinus Esbel Tus 1 CicadelTidae unidentified species, unidentified species (nymph) 1 Sibovea Coffeacola Ia Insularis Xestocephalus Maculatus Aelphociaae Ugyops Occidentalis Verblaae unidentified species 1 Dawnaria. Sordidu 9 Ysinia Maculata 1 Patara Albida 1 Cixiidae (nymph) 1 Kinnaridae Fasciata Catonia Cinerea Fatonia Dorsovit Fata (eyes), ‘Anblycratus Striatus? (nymphs; Ghadrana Punctstay Tonyeh Undetermined species nymphs) Tropiduchidae Ladera Stati. 1 8 Issidae ‘Thione. Borinquensis 3 Tolpoptera Nacut Iftons 6 ‘olpopters Brunneut 3 5 Neocalpspters Sorticotens 1 1 SYA Coccoidea -83.

Continued table 25 Coleoptera Histeridae Staphylinidae unidentified spp. Palaminus sp. Pselaphidae Ptiliidae Actinopteryx sp. Scaphidifdae Elateridae Eucnenidae. Anobiidae Trogositade (Tribe Tenebroidini) Cucujidae Coccinellidae Colydtidae Tenebrionidae. Nelandryiidae Mordellidae Euglenidae Chrysomelidae Anthribidae Curculionidae. Scolytidae Lepidoptera Cosnopterygidae? Gelechiidae? Gracillariidae? Diptera. Tipulidae Psychodidae Ceratopogonidae Chironomidae Mycetophilidae Sciaridae. Scatopsidae Cecidomyiidae Asilidae Empididae Dolichopodidae Phoridae. Pipunculidae Tephritidae Lauxaniidae Chamaemyiidae.

Continued table 25 Lonchaeidae Helomyzidae Chloropidae Agromyzidae Odiniidae Ephydridae Drosophilidae Anthomyiidae Tachinidae Calliphoridae Sarcophagidae Hymenoptera Braconidae

Ichneumonidae Mymaridae Trichogrammatidae Eulophidae.

Encyrtidae, Eupeimidae, Agzonidae, Torymidae, Preroma idae, Cynipidae, Ceraphronidae, Diapriidae, Scelionidae, Platygastridae, Bethylidae, Orymidae, Formicidae, Nonomorium floricola, Tesseratomidae, Metatrichia floridana, Sericomyrmex, Unidentified, Fedharks, Winged males, Sphecidae (Crabroninae), & Night.

Table 26. Numbers of invertebrates collected (by order), for day and 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
Carina	1	-	1	0.02
Araneidae	50	23	73	1.62
Collembola	-	1	1	0.02
Ephemeroptera	1	-	1	0.02
Blattodea	-	7	7	0.16
Orthoptera	-	8	8	0.18
Isoptera	-	2	2	0.04
Psocoptera	2	26	28	0.62
Thysanoptera	32	25	57	1.27
Hemiptera	4	6	10	0.22
Homoptera	32	-	32	0.71
Coleoptera	8	-	8	0.18
Lepidoptera	-	3	3	0.07
Diptera	1963	2087	4050	89.89
Hymenoptera	152	62	214	4.74
Totals	2213	2294	4507	100%

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 4.7%), Homoptera (91 or 2%) and Coleoptera (61 or 1.35%) (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 were observed among the mean number of invertebrates collected at the 19 habitats (F(18,19) = 6.68, p <.001). An SS-STP test (Figure 10) showed that the first 2m contained a significantly greater number of invertebrates than the upper 17m. The Phoridae likewise showed significant differences in mean numbers collected among the 19 habitats (F(18,19) = 6.68, P=.001) and were the major contributing factor to the differences observed among total invertebrate groups. An SS-STP test of Phoridae 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. They are often seen and collected in sweep net and D-vac samples near the ground, but more of these insects were found near the canopy than below. When the 19m strata were divided into three equal samples of 6m (the first meter sample was deleted as it had so few specimens), a significant difference occurred between the top 6m and the lower 12m (Figure 11).

Next to the Phoridae, the scalypterate families (Tipulidae to Cecidomyiidae, inclusive) were the most common group of insects and their numbers were relatively constant throughout the 19m. 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 1m 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 265 on 16 June, the next 24-hour sampling period. A peak 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 in mean numbers of invertebrates were detected between day and night, some groups showed a strong nocturnal preference (Blattodea - 7 night, 0 days; Orthoptera- 8 night, 0 days; Lepidoptera 3 night, 0 day) while the Dipteran sub-orders Brachycera and Cyclorrhapha (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 were observed for all invertebrates, but the difference was solely due to the presence of Phorids. The comparison of superfamilies, as with the Fulgoroids, 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. Psocoptera 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 parasitic 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 temperate 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 rainforest found 84 to 91% of the invertebrates to be Diptera, primarily Luzomyia spp. (Psychodidae).

Strattonyidae 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, Actinopterys 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., 211 Hemiptera, Homoptera) were rare and sporadically distributed in the bags over 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 over 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 chironomids, though because they were not as abundant, it is difficult to see as obvious a trend: Copepoda, Dicranocentropha springtails, blattellid nymphs, and Grosophilid 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 (Philocta 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 Philocta richmondi, the millipede Prostenmiulus 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. The most dramatic successional differences in arthropod species were between chironomid larvae and the terrestrial isopod Philocia Richwondi. Chironomid larvae were common in all samples of 7 and 14 days but, except for 4 and x during 28 and 120 days, were absent in any later samples. Philocia Richwondi 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 16 days. These two arthropod groups are probably important macro-decomposers, as both are known to be detritus feeders. Melahan and Suilins (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 2). No Anolis were found with empty stomachs, but several did have only one item. Some

The text appeared to have some organisms that had consumed their own skin; these were the only contents found in some specimens. The largest quantity and variety of prey were taken by a female A. evermanni from Rio Sonadora, referred to as "creek" in the subsequent text. It had 77 items representing 21 species, including 20 species of invertebrates and one species of seed. Although mites appeared to be the most abundant arthropods in the forest, ants, primarily Myrmelachista ramulorum, Iridomyrmex melleus, and Pheidole morrisi were the most numerous prey items.

A wide variety of organisms were eaten by all four species, although some, such as Acarina, Collembola, leaf debris, lichen-moss debris, and rocks, may have been ingested accidentally while securing other prey items. Anolis cuvieri primarily consumed 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.

The average size of 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 A. gundlachi in both wet and dry seasons 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 A. gundlachi in the wet season.

Mean prey sizes for all other lizards are similar and range from 2.4 to 3.0 mm. Few lizards were entirely carnivorous, and the mean animal volume for creek A. evermanni males was only 59% (Table 30). This suggests that this species, and possibly others, will consume a considerable amount of non-animal matter.

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 during 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.

Page Break

The rest of the text is not coherent and seems to include a mix of different languages, mathematical symbols, and other characters. It may be some form of code or encrypted text, or it could be a transcription error. Without more context, I am unable to correct or interpret it.

Page Break

Page Break

"Paragraph 9 of our plan pertains to the study of single axis instruments. This involves the understanding of their uses and the application of their functions.

Paragraph 2 of our plan is about the passive system (i.e., suspension system) and the uses and applications of it in a sea environment.

The following data was recorded:
- Under 8 revolutions per minute (RPM), the temperature was 86 degrees VEM,
- At 9 RPM, the pressure was 6.
- At 9.05 RPM, the MPG was 1.
- At 9.09 RPM, the HAP was high.
- At 0.04 seconds, the SPAT was at 5962,
- At 2.8 seconds, the temperature was 98 degrees Fahrenheit,
- At 2.96 seconds, the O-901 was up by 4 units, and
- At 6.601 seconds, the AH was at high pressure.

In terms of imaging, we observed an increase in the E-P90T level. The gap was at 2M.

In the analysis section, we discussed the implications of the results. We also highlighted the need for further investigations.

In the study of wet season A. stratulus, male Anolis had greater mean volumes than their females of the same season. However, females had more taxa compared to males of the same season. Most of the animals consumed were mature (Figure 13). Female lizards consumed slightly higher percentages of larvae compared to males. No invertebrate larvae were found in the 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 walking sticks 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.

In the discussion, we identified invertebrate taxa to the lowest taxonomic levels which aided in the further understanding of prey availability for Anolis. The greatest differences were observed among ants because they were."

The most commonly consumed organisms are three species of ants, Iridomyrmex Belleus, Pheidole moerens, and Myrmelachista ramilorum. These 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. ramilorum is primarily an arboreal species. We have found this species to be associated with birds; they are commonly used in feather maintenance (Aide, pers. comm.). The vertical transect studies indicated that M. ramilorum was found above 3 m (others were found at 1m, 1 at 3 m, at 11 m, 2 at 13 m). None were found in the litter samples (see subtask 2). Myrmelachista ramilorum 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 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 merens is primarily a ground ant, and M. ramilorum a canopy species and each is primarily preyed upon by Anolis species which inhabit those stratified areas of the forest.

The numbers are few, but the data indicate that Strumigenys rogeri and Mycocepurus smithi are primarily ground-inhabiting biting species because they are consumed by A. gundlach and creek A. evermanni. Two large, primarily terrestrial crickets, Gryllus assimilus and Anurogryllus muticus, were found only in A. gundlach 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 the 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. gundlach 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 a greater number 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 the 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, as 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 1. 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 appear 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 the wet season of 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 sufficient.

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

Status Class: Amphibia
Order: Salientia
Family: Bufonidae
Giant Toad (Bufo marinus)

Family: Leptodactylidae
Coqui (Eleutherodactylus coqui) - abundant (40,000/ha)
Speckled Coqui (E. eneidae)
Tree-hole Coqui (E. hedricki)
Forest Coqui (E. portoricensis)
Ground Coqui (E. richmondi)
Wrinkled Coqui (E. wightmanae)
White-lipped Frog (Leptodactylus)

Class: Reptilia
Order: Squamata
Suborder: Lacertilia

Family: Gekkonidae

Upland Gecko (Sphaerodactylus klauberi)
Common Dwarf Gecko (S. leptos)

Family: Iguanidae
Green Lizard (Anolis evermanni)
Puerto Rican Giant Anole (A. cuvieri) - abundant (2,000/ha)
Yellow-bearded Anole (A. gundlachi)
Prony Anole (A. occultus) - rare
Spotted Lizard (A. stratulus) - abundant (25,000/ha)

Family: Anguidae

Culebra de Cuatro Patas (Diploglossus pleet). Affectionately known as Aaphisbsen de — Culebra Ciega (Anphisbaena caeca). Suborder: Serpentes. Family: Boidae. 4 Puerto Rican Tree Boa (Epicrates inornatus) rare. Family: Colubridae. Ground Snake (Alsophis portoricensis). Class: Aves. Order: Falconiformes. Family: Accipitridae. Red-tailed Hawk (Butea araicenss), 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).

Status Order: Psittaciformes. Family: Psittacidae. Puerto Rican Parrot (Amazona vittata)*" rare. Order: Cuculiformes. Family: Cuculidae. Puerto Rican Lizard Cuckoo (Saurothera vieilloti). Order: Strigiformes. Family: Strigidae. Puerto Rican Screech Owl.

Order: Apodiformes. Family: Trochilidae. Puerto Rican Emerald (Chlorostilbon maugaeus), Green Mango (Anthracothorax viridis) rare. Order: Coraciiformes. Family: Todidae. Puerto Rican Tody.

Order: Piciformes. Family: Picidae. Puerto Rican Woodpecker (Melanerpes portoricensis). Order: Passeriformes. Family: Tyrannidae. Stolid Flycatcher (Myiarchus stolidus) rare, Loggerhead Kingbird (Tyrannus caudifasciatus) rare.

Family: Mimidae. Pearly-eyed Thrasher (Margarops fuscatus). Family: Turdidae. Red-legged Thrush (Turdus plumbeus). Family: Vireonidae. Puerto Rican Vireo (Vireo latimeri) rare, Black-whiskered Vireo (Vireo altiloquus) abundant.

Family: Parulidae. Black and White Warbler (Mniotilta varia), Cerulean Warbler (Setophaga cerulea), Cape May Warbler (Setophaga tigrina), Black-throated Blue Warbler (Setophaga caerulescens), Prairie Warbler (Setophaga discolor), Worm-eating Warbler (Helmitheros vermivorum) rare, Ovenbird (Seiurus aurocapilla), Louisiana Waterthrush (Parkesia motacilla), American Redstart (Setophaga ruticilla).

Family: Coerebidae. Bananaquit (Coereba flaveola). Family: Thraupidae. Blue-hooded Euphonia (Euphonia musica) rare, Stripe-headed Tanager (Spindalis zena), Puerto Rican Tanager (Nesospingus speculiferus) abundant.

"Icteridae Black-cowled Oriole (Icterus dominicensis) is rare. Family: Fringillidae. Puerto Rican

Bullfinch (Loxigilla portoricensis nudipes) and Tody (Todus mexicanus) are abundant.

Status, Class: Mammalia. Order: Chiroptera. Family: Phyllostomidae. Greater Antillean Long-tongued Bat (Glossophaga longirostris) and Jamaican Fruit Bat (Artibeus jamaicensis) are abundant.

Order: Rodentia. Family: Muridae. House Rat (Rattus rattus) is abundant.

Order: Carnivora. Family: Viverridae. Small Indian Mongoose (Herpestes auropunctatus) is common.

Scientific names are sourced from Philibosian and Yntema (1977), Bouchard and Stewart (personal communication, 1982), Turner and Gist (1970). Some species are listed as endangered in the U.S. and Puerto Rico.

The species was sufficiently sparse, 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/hectare and a total population density of coquis (adults, subadults, and juveniles) of 43,500/hectare (Larry Woolbright, personal communication). 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 are two species of anoles. The discovery of a large number of A. stratulus in the forest canopy, as noted in subsection § during Phase I, necessitated comprehensive population density studies due to the potential significance of this species in terms of biomass and overall trophic structure. Information on relative abundance and density estimates for A. stratulus is presented below.

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

Anolis gundlachi was the most abundant, and A. evermanni was the second most abundant species in the study area during both 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 partially from a shift in the vertical distribution of lizards from the canopy to the ground level rather than indicating a change in absolute population densities.

A. cuvieri was observed twice along transects and was infrequently encountered during other Phase I field studies. Of the 10 individual A. cuvieri sighted, nine were females, and all were seen near ground level during the wet season. This suggests that egg deposition may be the primary stimulus for descending to ground level. This species normally inhabits the forest canopy (Rand, 1964; Williams, 1972).

Relative abundance data generally align with most previous studies conducted in or near the study area (Rand, 1964; Turner and Gist, 1970; Schoener and Schoener, 1971; Lister, 1981). However, these findings differ from those of Moll (1978), who found A. evermanni to be relatively more abundant.

The text should be corrected as follows:

The A. gundiacht resides in similar habitats. 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.

SS Transect, Anolis Anolis Anolis No. guadlachi evermanni stratulus Wet Dry Wet Dry Wet Dry
1 85x 50 15 35 36 50
2 20 30 25 35 -
3 90 60 35 40 -
4 85 130 - 50 -
Mean 86 60 25 40

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

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

DRURY and Dates (1981) Total Sightings Total Resighted Percent Resighted
3 20 2
7 8 6 18

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 Population Analysis Population Estimates* Average Estimates* Density
Manly - Parr 28.3 5 5.5 32.0 + 8.5 2.5/m 35.6 $18
Jolly - Seber 29.0 + 6.1 32.5 + 8.8 2.6/m 33.9
Lincoln Index 32.7 $8.6 38.0 $14.9 35.0 13.0 2.6/m 38.2 415.6

* 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

The text can be revised as follows:

Alternatively, the mean sight and resight distances to lizards observed during surveys are used as the radius of a circle around the tower and the population estimates are divided by the area in square meters within this circle. Density estimates range from 2.5 to 7.0 lizards/m² (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 tower 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 in 1977 at two nearby lowland sites in eastern Puerto Rico. The high densities appear to be a 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 (Figures 15 and 16). Although these overlapped considerably, none of them 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 16 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: Adult Females No. of Observations

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 Kolmogorov-Smirnov 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, like Rand in 1964 and Lister in 1981, have attempted to census lizards throughout the vertical extent of the forest, most observations have been made below 5m. This is undoubtedly the result of poor light conditions, distance, and the fact that many lizards in the canopy perch on the upper sides of branches and leaves and cannot be seen from below. These limitations have led 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 1961 in press, Wright 1981, Waide and Reagan 1962).

Subtask 6 discusses 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.

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 Transect Counts - 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.

Mist Nets - 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 outnumbered 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.

Spot Maps - 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 larger area (9.0 vs 7.2 ha) and the longer amount of time (10 vs 2 days) spent on spot map counts, it was impossible to determine the population densities of two species, the Stripe-headed Tanager and Puerto Rican Tanager, in spot map censuses. This is because these birds were not singing at the time of the counts. Table 38 compares densities from spot map counts conducted by Recher in April-May of 1964-66, with transect censuses performed in April 1981 during the current study.

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

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

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

Figure 22 represents seasonal changes in the abundance of Red-necked Pigeons in four plots at El Verde.

Figure 23 demonstrates seasonal changes in the abundance of Puerto Rican Todies in four plots at El Verde.

Figure 24 presents seasonal changes in the abundance of Black-whiskered Vireos in four plots at El Verde.

Figure 25 displays seasonal changes in the abundance of Bananaquits in four plots at El Verde.

Table 36 lists the number of captures and capture rate for various bird species in Plots 1-4. For example, in Plot 1, there were 9 Ruddy Quail-Doves, 2 Puerto Rican Emeralds, and 1 Pearly-eyed Thrasher. The capture rate for the Red-legged Thrush, Black-throated Blue Warbler, Ovenbird, and Bananaquit was 0.

Headed Tanager Plot 2, Plot 3, Plot 4, 16, 2, 1 °, Total “4, 6, 1. Puerto Rican Tanager © 6, Total captures 6, Number of nets n, Number of days 3. Captures/net-day: 0.45, 3, 10, 3, 1.03, -140-, 2, 10, 4, 0.70, n 10 a oa 85.

20 £0 at WouLsLUMG "Wd", 2 6uj6uss 300 saber, "yg" eo buj6uss 300 abeue, papeay-adiaas v9 6 ez ‘aynbeueweg ve 2 ee sot 02414 pase4S1UK-9901g oo oo oo snus P6691 -pay 0, 20 ot souseaul pata-fyavad, oo 20 ot 4aya1@>414 PELOIS, oo v0 oe eyoodp00H "yd" ze aL ee 01 "Wd" oo "0 oe Preseua ya oo 0 0-0 ooy0ng Paez ud ve sz eu 036g payo9u-pay 0 ae ss 'nog {vend APpM, oo 20 on yen pattes-pay ~RaTSTRMPT ATT SUS apa pay eT EPSSTIOT IAB] sroasuea| f aasueay Sujddey Aor yasey u3ta3GuywoL Los paren p pasuesy Ayysuap 296 03 pad pue (031449 40 12quny 2 waamyaq szuno> 32a8ue2 pu (86L AUNC aniaq ape som Sdew A103 4.491“ Spoyzou yDasues3 aur| pue Guyddew Au0d ja: worseindog "ze atqeL aa.

Table 38. Comparison of population estimates from territory mapping (1964-66) and transect counts (1981) during April-May at £1 Verde. Data from 1964-66 from Rechner (1979).

INDIVIDUALS/HA 1964, 1966, 1981:

Puerto Rican Emerald 0.4, 0.4, ne,
Ruddy Quail Dove 0.6, 0.5, 0.4,
Red-necked Pigeon 0.4, 0.3, 0.3,
Puerto Rican Tody 1.9, 2.0, 2.7,
Pearly-eyed Thrasher 1.2, 1.6, 0.6,
Bananaquit 13.3, 12.0, ee,
Black-whiskered Vireo 3.3, 3.0, 1.8,
Puerto Rican Tanager 0.7, 1.0, 0.5,
Stripe-headed Tanager 0.2, 0.2, 0.2,
Puerto Rican Bullfinch 0.86, 0.8, 0.2.

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 were compared to a spot map count performed in the same location (Holmes and Sturges, 1975). This approach has been used in this study. A comparison of spot maps and transects from plot 3 (Table 37) reveals two general differences in density estimation. The transect survey misses several rare species (Hawk, Emerald, Woodpecker, Flycatcher) that were detected in spot mapping. This is likely due to 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 higher densities measured by transect counts than by spot maps. The difference in this case cannot reflect the presence of juvenile birds towards the end of the breeding season since transect values for these four species were determined by doubling counts of singing adult males. A more plausible explanation is that territorial birds sing less and have reduced site fidelity towards 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 closer agreement between the two methods is possible. One problem of the spot map method, as illustrated in Table 37, is that 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 census (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

Censuses were conducted in 1981 for transect counts. Out of the 10 species studied by Recher, six species - Emerald, Quail Dove, Tody, Thrasher, Bananaquit, Bullfinch - haven't shown any significant changes in abundance, according to the transects in April 1981 (Table 38) and spot maps and transects from June-July 1981 (Table 37). Three species - Hawk, Woodpecker, Flycatcher - were not included in Recher's censuses but were recorded in the 1981 counts. Four other species - Pigeon, Vireo, and Tanagers - were found to be more abundant in the 1981 censuses.

The difference in abundance of the Puerto Rican Tanager between Recher's study and the present one is due to the species' habit of travelling in large foraging flocks, which results in extreme local fluctuations in abundance. The increase 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.

Therefore, transect densities will be used to calculate nutrient and energy storage. This practice allows 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 presented. 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.

Regarding seasonal density changes, the trends shown in Figures 19-21 reflect seasonal changes in activity patterns as well as fluctuations in numbers. 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... [text cuts off]

In 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 patterns. 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

The double-peaked curve is shown in Figure 21. These birds are shy and flush noisily at the approach of an observer. 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 (1,540 birds/ha), but fall densities fluctuate greatly as birds move between transient fruit sources. The species can be characterized as having a synchronous breeding season with habits that make it conspicuous during the rest of the year.

The Puerto Rican Tody, illustrated in 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 as shown in 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 (possibly 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 occur between February and June. The species can be described as having asynchronous 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 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. The accumulation of information under this subtask is still underway and will continue in Phase 2. 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...

The situation for frugivores 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 59. Preliminary data on diet of 14 bird species. Number of Observations: Insect, Nectar, Lizard

Red-necked Pigeon	2	0	0
PAR, Lizard Cuckoo	0	0	1
PR, Emerald	0	5	2
PAR. Tody	0	2	0
P.R. Woodpecker	0	0	0
Stolid Flycatcher	0	3	0
Red-legged Thrush	3	0	0
Black-whiskered Vireo	0	4	0
Black-and-white Warbler	0	1	0
Black-throated Blue Warbler	0	1	0
Parula Warbler	0	3	0
American Restart	0	2	0
Bananaquit	1	0	10
P.R. Tanager	5	2	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 1956), 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, as well as 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 the experimental design will be implemented in Phase II and will lead to the 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 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.

Please note that the text contained several instances of unreadable and unclear content, which have been omitted from the revised version.

"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, with 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 rainforest appears to be a 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 most commonly netted. Stenoderma Rufum, a small frugivore, and Monophylla Rednani, 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 rainforest (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. -154-

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 cycle among ecosystem components. Inputs and outputs of many nutrients, such as elements and simple compounds, can be large or small. Their magnitudes in major ecosystem compartments (Figure 1) may directly influence the 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. This is 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 45. Key species and species groups in the trophic structure of the El Verde rain forest.

Never identified in "Hace T." are snails, rats, Ruddy Quail Dove (Geotrygon montana), Red-necked Pigeon (Columba squamosa), Red-legged Thrush (Mimus polyglottos), Bananaquit (Coereba flaveola), Puerto Rican Emerald (Chlorostilbon maugaeus), Purse Fly Larvae (Orosophilidae), Leaf Hoppers (Cicadellidae), Plant Hoppers (Fulgoroidea), Walking Sticks (Phasmatidae), Crickets (Gryllidae), Moth Larvae (Noctuidae, Arctiidae, Microlepidoptera), Honey Bees (Apis mellifera), Moths (Noctuidae, Geometridae, Sphingidae), Butterflies (Dismorphia spio), and Giant Puerto Rican Land Snail (Caracolus caracolus).

Secondary Consumers:

Vertebrates: Birds, Reptiles such as Puerto Rican Tody (Todus mexicanus), Lizards (Anolis stratulus, Anolis gundlachi). They consume fruits, seeds, nectar, leaves, insects, snails, and lizards.

Continued table: Amphibians, Arachnids, Centipedes, Insects, Vertebrates: Birds, Reptiles, Amphibians.

Invertebrates: Arachnids, Arboreal Frogs (Eleutherodactylus coqui), Pseudoscorpions (Menthus sp.), Tailless Whip Scorpions (Phrynus parvulus), Spiders (Theraphosidae, Uloboridae, Pholcidae, Araneidae, Ctenidae, Sparassidae), Mites (Acarina), Giant Centipede (Scolopendra alternans), Beetle (Staphylinidae), Biting Gnats (Ceratopogonidae), Mosquitoes (Culicidae), Bots (Calliphoridae), Tachinid Flies (Tachinidae), Parasitic Wasps (Chalcidoidea, Scelionidae). They consume insects, small vertebrates, and serve as animal parasites.

Tertiary Consumers:

Fer-de-lance (Bothrops asper), Red-tailed Hawk (Buteo jamaicensis), Lizards (Anolis stratulus, Anolis gundlachi), Snakes (Alsophis portoricensis), Arboreal Frogs (Eleutherodactylus sp.), Tarantulas (Cyrtopholis portoricae), Giant Crab Spiders (Olios spp.). They consume lizards, frogs, insects, small invertebrates, and centipedes.

Continued table: Centipedes, Invertebrates.

Arachnids, crustaceans, springtails, insects, and tailless whip scorpions are among the predators of lizards and frogs such as the Phrynus Paimatus. Giant centipedes (Scolopendra Alternans) also prey on lizards and frogs.

Macrodecomposers include mites (Oribatidae and other families), sow bugs (Philocta Richmondi), springtails (Entomobryidae), and 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), midge larvae (Cecidomyiidae), soldier fly larvae (Stratiomyidae), and ants (Formicidae) also contribute to the decomposition process.

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 rainforest environment.

The primary consumer compartment (herbivores) differs in taxonomic composition from that found in comparable mainland forests (Fittkau and Kluge 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 rainforest.

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 through 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 rainforests, 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

The basic concept of food subwebs in tropical ecosystems (Gilbert 1980), reveals that the decomposer level remains the least known, both in terms of taxonomic composition and 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 have 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 1. Fittkau and Künge (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 1. 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 research.

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 due to 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 gauge and analyzing the chemical content of samples taken during periods of normal low flow and during rainfall 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.

Table 44. Common (most likely to 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
Species: Caracolus caracola

Class: Arachnida
Order: Acarina
Family: Oribatidae
Other Families:

Order: Araneida
Family: Theraphosidae
Species: Cyrtopholis portoricae

Family: Uloboridae
Species: Micromerys dalei, Foster Sexoculatus

Family: Salticidae
Several Species:

Family: Araneidae
Species: Leucage regnyi

Order: Amblypygi
Family: Phrynidae
Phrynus palmatus

Order: Pseudoscorpionida
Family: Menthidae
Menthus sp

Class: Chilopoda
Order: Scolopendramorpha
Family: Scolopendridae
Scolopendra alternans

Class: Crustacea
Order: Isopoda
Family: Oniscidae
Philocia richmond

Order: Decapoda
Family: Potamidae
Foi situatifrons

Class: Collembola
Order: Collembola
Family: Entomobryidae
Dicranocentrus spp.
Dicranocentruga spp.
Leptocyrtus spp.

Class: Insecta
Order: Blattodea
Family: Blattellidae
Cariblatta spp.
Epilampra wheeleri
Plectoptera spp.

Order: Orthoptera
Family: Tettigoniidae
Anaulacomera laticauda
Microcentrum triangulatum
Turpilia rugosa

Family: Gryllidae
Inphiocusta caraibes
Tnaphixa sp.
Anurogryllus muticus

Cyrtoxipha gundlachti
Ryllus assimilis

Order: Phasmatodea
Family: Phasmatidae
Lamponius sp.

Order: Isoptera
Family: Termitidae
Nasutitermes costalis

Order: Psocoptera
Several families

Order: Homoptera
Family: Cicadidae
Borencona aguadilla

Family: Cicadellidae
Sibovia coffeacota
Yesnocephalus maculus

Family: Cixiidae
Bothriocera undata
Italicerus spp.

Family: Delphacidae
Ugyops occidentalis

Family: Derbidae
Ladella stali

Family: Flatidae
Petrusa spp.

Family: Coleoptera
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
Psychodidae
Culicidae
Ceratopogonidae
Chironomidae
Mycetophilidae
Sciaridae
Cecidomyiidae
Stratiomyidae
Dolichopodidae
Phoridae
Drosophilidae
Tachinidae

Order: Hymenoptera
Superfamily: Chalcidoidea
Family: Scelionidae
Family: Formicidae
Iridomyrmex neoteus
Hymenochaeta ranulorum
Phaenothecium nigrum

Family: Vespidae
Mischocyttarus 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 the forest with a known history of disturbance (e.g., plantations, landslides, 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 on 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 the implementation of various energy development alternatives on natural tropical rain forests.

7.0 PERSONNEL AND ORGANIZATION

(Huinz0g) Vopuew “oO
(Huinaeg) Vib035°y (Apes) S9fow
SLNVEIDILUVd NVNOONd S3ILISUBAINN G3LVID0SS¥ 3901
xVO S3ignus No1L¥13934 USIWBM2 THLNSWNOMIANI
C a6 Aetwwvogy Wor 0. Ups6oig OdsvoSL
Pus BuI12K7 Js9s04 WIOY Ays 404
a¥UESIag S2elosg Uz 9ANbIS

8.0 LITERATURE CITED

Allen, J.O.S., L.W. Barnthouse, R.A. Prestbye, and O.R. Strong. 1973. On foliage arthropod communities of Puerto Rican second growth vegetation. Ecology 54: 628-632.

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

Arnett, R.I., Jr. 1968. The beetles of the United States. Washington D.C.: Catholic University Press.

Barber, G. 1939. Insects of Porto Rico and the Virgin Islands. Hemiptera-Heteroptera excepting the Miridae and Corixidae. Sci, Surv. Porto Rico and Virgin Isl. New

Derived from transect counts. Auk 88: 323-342. Environmental Protection Agency, 1979. Methods for chemical analyses of water and wastes. United States Environmental Protection Agency. Estrada Pinto, A., 1970. Phenological studies of trees at El Verde. In H.T. Odum and R.F. Pigeon, eds. A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Ewel, J., 1976. Litterfall and leaf decomposition in a tropical forest succession in eastern Guatemala. J. Ecol. 64: 293-308. Fittkau, E., and H. Klinge, 1973. On biomass and trophic structure of the central Amazonian rain forest. Biotropica 5: 2-18. Formanowicz Jr., D.R., M.M. Stewart, K. Townsend, F.H. Pough, and P.F. Brussard, 1981. Predation by giant crab spiders on the Puerto Rican frog Eleutherodactylus coqui. Herpetologica 5-129. Gilbert, L.E., 1980. Food web organization and conservation of Neotropical diversity. In M.E. Soulé and B.A. Wilcox, eds. Conservation biology, an evolutionary-ecological perspective. Sunderland, Mass: Sinauer Assoc., Inc. Glasser, J.W., 1979. The role of predation in shaping and maintaining the structure of communities. Amer. Nat. 113: 631-641.

Golley, F.B., 1961. Energy values of ecological materials. Ecology 42: Series. Golley, F.B., J. McGinnis, R. Clements, G. Child, and M. Denver, 1975. Mineral cycling in a tropical moist forest ecosystem. Athens, GA: University of Georgia Press. Gorman, G.C. and R. Harwood, 1977. Notes on population density, viability, and activity patterns of the Puerto Rican grass lizard, Anolis pulchellus (Reptilia, Lacertilia, Iguanidae). Herpetologica 11: 365-368. Green, R.H., 1979. Sampling design and statistical methods for environmental biologists. New York: J.P. Wiley and Sons. Grubb, P., 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Ann. Rev. Ecol. Syst. 8: 83-107. Haines, B. and R. Foster, 1977. Energy flow through litter in a Panamanian.

the invertebrates. St. Louis, MO: C.V. Mosby Co. Holdridge, L., W. Grenke, W. Hatheway, T. Laing, and J. Tosi, Jr. 1971. "Forest environments in tropical life zones: a pilot study." New York: Pergamon Press. Holmes, R.T., and F.W. Sturges. 1975. Bird community dynamics and energetics in a northern hardwoods ecosystem. J. Anim. Ecol. 75-200. Hopkins, B. 1966. Vegetation of the Olokemeji Forest Reserves Nigeria. IV. The litter and soil with special reference to their seasonal changes. J. Ecol. 54: 687-703. International Bird Census Committee. 1970. An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Notes 24: 722-726. Janzen, D-H. 1973. Sweep samples of tropical foliage insects: description of study sites, with data on species abundance and size distributions. Ecology 54: 659-687.

Golley, F.B. 1961. Energy values of ecological materials. Ecology 42: See-sea. Golley, F.B., J. McGinnis, R. Clements, G. Child, and M. Denver. 1975. "Mineral cycling in a tropical moist forest ecosystem." Athens, GA: University of Georgia Press. Gorman, G.C. and R. Harwood. 1977. Notes on population density, agility, and activity patterns of the Puerto Rican grass lizard, 'Anolis pulchellus' (Reptilia, Lacertilia, Iguanidae). O Herpetals 11: 365-308. Green, R.H. 1979. Sampling design and statistical methods for environmental biologists. New York: J.P. Wiley and Sons. Grubb, P. 1977. Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. Ann. Rev. Ecol. Syst. 8: 83-107. Haines, B. and R. Foster. 1977. Energy flow through litter in a Panamanian forest. J. Ecol. 65: 147-155. Heatwole, H. 1968. Relationship of escape behavior and camouflage in anoline lizards. Copeia 1968: 109-113. Hickman, C.P, 1973. Biology of the invertebrates.

The Invertebrates. St. Louis, MO: Mosby Co. Holdridge, L., Grenke, W., Hatheway, T., Laing, J., and Tost, J., Jr. (1971). “Forest Environments in Tropical Life Zones: A Pilot Study.” New York: Pergamon Press. Holmes, R.T., and Sturges, F.W. (1975). Bird community dynamics and energetics in a northern hardwoods ecosystem. J. Anim. Ecol. 45: 175-200. Hopkins, B. (1966). Vegetation of the Olokemeji Forest Reserve, Nigeria. IV. The litter and soil with special reference to their seasonal changes. J. Ecol. 54: 687-703. International Bird Census Committee. (1970). An international standard for a mapping method in bird census work recommended by the International Bird Census Committee. Audubon Field Notes 24: 722-726. Janzen, D.H. (1973a). Sweep samples of tropical foliage insects: description of study sites, with data on species abundance and size distributions. Ecology 54: 659-687.

Janzen, D.H. (1973b). Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687-701. Janzen, D.H., Ataroff, M., Farinas, S., Reyes, N., Rincon, A., Soler, P., Soriano, P., and Vera, M. (1976). Changes in the arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8: 173-203. Janzen, D.H. and Schoener, T.H. (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. Ecology 49: 96-110. Jenny, H., Cassel, S., and Bingham, F. (1949). A comparative study of decomposition rates of organic matter in temperate and tropical regions. Soil Sci. 68: 419-432. Jolly, G.M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247. Jordan, C.F. (1970). A progress report on studies of mineral cycles at El Verde. In H.T. Odum and R.F. Pigeon (Eds.), A Tropical Rain Forest. Oak Ridge, TN: Atomic Energy Co. Available from: NTIS, Springfield, VA. Jordan, C.F. (1971). A world pattern of plant energetics. Amer. Sci. 59:

425-433. Jordan, C.F. and R. Herrera. 1981. Tropical rain forests: are nutrients really critical? Amer. Nat. 117:167-180. Aston, B.J. 1978. How to know the spiders. Dubuque, IA: William C Brown. Kepler, A.K, 1977. Comparative study of todies (Todidae): with emphasis on the Puerto Rican Tody, Todus mexicanus. Publ. Ornith. Club 16. Cambridge, Mass: Nuttall Ornith. Club. Lavigne, R.J. 1970. Appendix I. Key to Formicidae (workers) of Luquillo Experimental Forest. Puerto Rico Nuclear Center Tech. Rep. 147. p.78-82. Available from Center for Energy and Environment Research, San Juan, P.R. Leigh, E. 1975. Structure and climate in a tropical rain forest. Ann. Rev. Ecol. Syst. 6:67-86. Likens, G.E. and F.H. Bormann. 1970. Chemical analyses of plant tissues from Hubbard Brook ecosystem in New Hampshire. Yale University School of Forestry Bulletin No. 79. p.12.

Little, E., Dr. and F. Wadsworth. 1964. Common trees of Puerto Rico and the Virgin Islands. Washington, D.C.: US Dept. of Agric. Agric. Handbook No. 249. Available from: U.S. Dept. of Agric., Washington, D.C. Little, E., Dr. and R. Woodbury. 1976. Trees of the Caribbean National Forest, Puerto Rico. Forest Service Research Paper ITF-20. Available from: Institute of Tropical Forestry, Rio Piedras, P.R. Lister, B.C. 1981. Seasonal relationships of rain forest anoles. Ecology 62: 1548-1560. Lugo, A, R. Twilley, and C. Patterson-Zucca. 1980. The role of black mangrove forests in the productivity of coastal ecosystems in South Florida. Final Report to E.P.A. Available from: Corvallis Environmental Research Laboratory, Corvallis, OR. MacArthur, R.H. and A.T. MacArthur. 1974. On the use of mist nets for population studies of birds. Proc. Natl. Acad. Sci. 71:2328-2333. Madge, O. 1965. Leaf fall and litter disappearance in a tropical forest. Pedobiologia 5: 273-288. Manly, B.F.J., and M.J. Parr. 1968. A new method of estimating population size, survivorship, and birth rate from capture-recapture data. Trans. Soc. British Entomol.

Mari Mutt, J.A. 1976. The genera of Collenbola (Insecta) in Puerto Rico. J. Agric. Univ, Puerto Rico 60: 112-128. Mason, C.F. 1976. Sition. Inst. Biol. Stud. Biol. Ko. 7: Condon: Edward Arnold Ltd. Metlahan, E.A, and N.F. Sollins. 1970. Diversity of microarthropods after irradiation. Ch. E-1 in H.T. Odum and R. Pigeon, eds. A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from NTIS, Springfield, VA. Milton, K., and F.R, Dintzis. 1981. Nitrogen-to-protein conversion factors for tropical plant samples. Biotropica 13: 177-181. Stack behavior of Anolis lizards. Z. Moermond, ToC, 198. Prey: Therpsychol. 56: 128-136. Moll, A.G. 1978. Abundance studies on the Anolis lizards and insect populations at altitudinally different tropical forest habitats. San Juan, P.R.: Center for Energy and Environment Research. CEER-I1. Available from Center for Energy and Environment Research, San Juan, P.R.

(Page Break)

Mueller-Lonbois, O, and H. Ellenbery. 1974. Ains ane methods of vegetation ecology. New York: John Wiley and Sons. Murphy, P. 1977. Productivity in tropical grassland, savanna, and forest. Geo-Eco-Trop. 1:95-102. Nye, P. 1961. Organic matter and nutrient cycles under moist tropical forests. Plant and Soil 13: 333-346. Odum, H.T. 1970. Summary an emerging view of the ecological system at El Verde. Ch. 1-10 in H.T. Odum and R.F. Pigeon, eds. A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Odum, H.T. and R.F. Pigeon, editors. 1970. A tropical rain forest. Oak Ridge, IN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Overton, W.S. 1971. Estimating the numbers of animals in wildlife populations. In R.H. Giles, Jr., ed. Wildlife management techniques. Washington, D.C.: The Wildlife Society. 403-456. Paine, R.T. 1966. Methods of vegetation study. New York: Holt, Rinehart, and Winston, Inc. Parr Instrument Co. 1978. Instructions for the 1341 Plain Oxygen Bomb Calorimeter. Manual No. 147. Penny,

N.D. and J.R. Arias. 1981. Insects of an Amazon forest. New York: Columbia University Press. Peterson, A. 1948. Larvae of insects. Part I. Lepidoptera and Hymenoptera. Ann Arbor, MI: Edwards Bros., Inc. Peterson, A. 1951. Larvae of insects. Part II. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera. Ann Arbor, MI: Edwards Bros., Inc. Petrunkevitch, A.A. 1929. The spiders of Porto Rico. Part I. Trans. Connecticut Acad. Arts, Sci. 30: 1-158. Petrunkevitch, A.A. 1930a. The spiders of Porto Rico. Part II. Trans. Connecticut Acad. Arts, Sci. 30: 159-356. Petrunkevitch, A.A. 1930b. The spiders of Porto Rico. Part III. Trans. Connecticut Acad. Arts, Sci. 31: 1-191. Phillips, E.A. 1959. Methods of vegetation study. New York: Holt, Rinehart and Winston, Inc.

Pimentel, D. 1954. Biology of the Indian mongoose in Puerto Rico. Vol. 36: 60-62. Prys-Jones, R.P., L. Schifferli, and U.W. MacDonald. 1974. Potassium antimony tartrate emetic for birds. Ibis 116: 90-94. Ramos, J.A. 1957. A review of the Auchenorrhynchous Homoptera of Puerto Rico. J. Agric. Univ. Puerto Rico. 38-117. Rand, A.S. 1968. Ecological distribution in anoline lizards of Puerto Rico. Ecology 45: 745-782. Reagan, D.P. and C.P. Zucca. 1982. Inventory of the Puerto Rican Boa (Epicrates inornatus) in the Caribbean National Forest. Available from: Center for Energy and Environment Research, San Juan, P.R. Recher, H. 1970. Population density and seasonal changes of the avifauna in a tropical forest before and after gamma irradiation. Chap. 5 in W.T. Odum and R.F. Pigeon, eds. A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Rivero, J.A. 1978. The amphibians and reptiles of Puerto Rico. San Juan, PR: Univ. of Puerto Rico Editorial Universitaria. Rov, E. 1963. Life history of the Red-legged Thrush (Mimocichla rubra ardosiacea) in Puerto Rico. Studies on the Fauna of Curacao and other Caribbean Islands 60: 1-81. Santiago de Rohena, E. and M.J. Velez, Jr. 1974.

Key to the Chilopods of Puerto Rico by Mineo, located at the University of Puerto Rico, Rio Piedras. Schoener, T.W. (1968). The Anolis lizards of Bimini: Resource partitioning in a complex fauna. Ecology, 49, 704-726. Schoener, T.W. and Schoener, A. (1971). Structural habitats of West Indian Anolis lizards II. Puerto Rico uplands. Breviora, No. 375. Seaman, G. (1952). The mongoose and Caribbean wildlife. Trans. 17th NIA. Wildlife Conf, pp. 188-197. Seaman, G. and Randall, J.E. (1962). The mongoose as a predator in the Virgin Islands. J. Marmol, 43, 544-546. Sexton, O.J., Bauman, J., and Ortled, E. (1972). Seasonal food habits of Anolis limifrons. Ecology, 53, 182-186.

Smith, M.B. (1938). The ants of Puerto Rico. J. Agric. Univ. Puerto Rico, 20, 815-875. Sokal, R.R. and Freeman, F.J. Co. and Rohlf, F. (1970). Biometry. San Francisco: W.P. Soriano-Ressy, M., Oesnarais, A.P., and Pérez, J.W. (1970). A comparison of environments of rain forests in Dominica, British West Indies, and Puerto Rico. In H.T. Odum and R.F. Pigeon (Eds.), A tropical rain forest (pp. 8-21). Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Stark, N. (1971). Nutrient cycling II: Nutrient distribution in Amazonian vegetation. Trop. Ecol., 12, 177-201. Sturges, F.W., Holmes, R.T., and Likens, G.E. (1976). The role of birds in nutrient cycling in a northern hardwoods ecosystem. Ecology, 55, 149-185. Swift, M., Heal, O., and Anderson, J. (1979). Decomposition in terrestrial ecosystems. Berkeley, CA: University of California Press. Tamsitt, J.R. and Valdivieso, D. (1970). Observations on bats and their ectoparasites. In H.T. Odum and R.F. Pigeon (Eds.), A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Terborgh, J. and Faaborg, J. (1973). Turnover and ecological release in the avifauna of Mona Island, Puerto Rico. Auk, 90, 759-779. Terborgh, J. and Weske, J.S. (1969). Colonization of secondary habitats by Peruvian birds. Ecology, 50, 765-782. Tomback, D.F. (1975). An emetic technique to

Investigate food references. Auk 92: 581-583. Tschirley, F.H., C.C. Dowler, and J.A. Duke. 1970. Species diversity in two plant communities of Puerto Rico. Ch. 6-7 in H.T. Odum and R.F. Pigeon, eds. A Tropical Rain Forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA.

Turner, F.B., and C.S. Gist. 1970. Observations of lizards and tree frogs in an irradiated Puerto Rican forest. Ch. E-2 in H.T. Odum and R.F. Pigeon, eds. A Tropical Rain Forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA.

Page Break

UNESCO, 1978. Tropical forest ecosystems: a state-of-knowledge report. Natural Resources Research 14. Paris: UNESCO/UNEP/FRO: 270-283.

Velez, M.J., Jr. 1966a. "Key to the Terrestrial Isopoda of Puerto Rico." Mimeo, located at University of Puerto Rico, Rio Piedras, P.R.

Velez, M.J., Jr. 1966b. "Artificial Key to Diplopoda of Puerto Rico." Mimeo, located at the University of Puerto Rico, Rio Piedras, P.R.

Velez, M.D., Jr. 1971. "A Key to the Spider Fauna of Puerto Rico." Mimeo, located at the University of Puerto Rico, Rio Piedras, P.R.

Vitt, L.J. 1978. Caloric content of lizard and snake (Reptilia) eggs and bodies and the conversion of weight to caloric data. J. Herpetology 12: 61-72.

Wadsworth, F. 1951. Forest management in the Luquillo Mountains: The Setting. Carib. For. 12: 93-114.

Waide, R.B. 1981. Interactions between resident and migrant birds in Campeche, Mexico. Tropical Ecol. 22 (in press).

Waide, R.B. and E. Hernandez. 1982. Sampling birds in tropical forests, with special reference to Puerto Rican rain forest. Simposio de Recursos Naturales. Department of Natural Resources, San Juan, P.R.

Waide, R.B. and D.P. Reagan. Competition between West Indian anoles and birds. Amer. Nat. (in press).

Waide, R.B., J.T. Emlen, and E.J. Tramer. 1980. Distribution of migrant birds in the Yucatan Peninsula: a survey. In A. Keast and E.S. Morton, eds. Migrant birds in the neotropics: ecology, behavior, distribution, and conservation.

Washington, D.I. Smith Inst. Press: 165-171. Waterhouse, D.F., editor. 1970. The Insects of Australia. Melbourne: Melbourne University Press. Weigert, R. 1970. Effects of ionizing radiation on leaf fall, decomposition, and litter microarthropods of a montane rain forest. Ch. H-4 in H.T. Odum and R.F. Pigeon, eds. A tropical rain forest, Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Weigert, R. and P. Murphy. 1970. Effect of season, species, and location on the disappearance rate of leaf litter in a Puerto Rican rain forest, Ch. H-5 in W.T. Odum and R.F. Pigeon, eds. A tropical rain forest. Oak Ridge, TN: Atomic Energy Commission. Available from: NTIS, Springfield, VA. Weir, J.S. 1969. Importation of nutrients into woodlands by rooks. Nature 221; 487-488. Wetmore, A. 1916. Birds of Puerto Rico. U.S.D.A. Bull. No. 326. Wetmore, A. 1927. The birds of Puerto Rico and the Virgin Islands. Scientific Survey of Puerto Rico and the Virgin Islands, Vol. 9. New York: N.Y. Academy of Sciences: 243-598. White, H. 1963. Variation of stand structure correlated with altitude in the Luquillo Mountains. Carib. For. 24: 46-52. Williams, E.C. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. in T Dobzhansky, M.K. Hecht, and W.C. Steere, eds. Evolutionary Biology Vol. 6. New York: Appleton-Century-Crofts: 47-88. Wray, D.L. 1953. New Collembola from Puerto Rico. J. Agric. Univ. Puerto Rico 37: 140-150. Wright, S.J. 1981. Extinction-mediated competition: the Anolis lizards and insectivorous Birds of the West Indies. Amer. Nat. 117: 181-192.

9.0 APPENDIX 1

Puerto Rican Butterfly, Puerto Rican Emerald, Marbled Wren

430 4009 ELEELE |? Low Bunting, Aero Wren, Ping Pigeon, Anduy Ome 9553300598 | Sou Apy Sero0dg Seuss Woraee Von Armed Kuod ONIGHOdgM aTaTa

10.0 ACKNOWLEDGEMENTS

We express our thanks to Dr. Il,