PRNC—147 PUERTO RICO NUCLEAR CENTER ‘THE RAIN FOREST PROJECT ANNUAL REPORT June 1970 ‘OPERATED BY UNIVERSITY OF PUERTO RICO UNDER CONTRACT NO. AT (40-1)-1839 FOR U.S. ATOMIC ENERGY COMMISSION ---Page Break--- ---Page Break--- PRNC—147 BIOLOGY AND MEDICINE (710-4500) PUERTO RICO NUCLEAR CENTER ‘THE RAIN FOREST PROJECT ANNUAL REPORT Richard G. Clements, George E. Drewry and Robert J. Lavigne June 1970 ‘OPERATED BY UNIVERSITY OF PUERTO RICO UNDER CONTRACT NO. AT (40-1)-1829 FOR U.S. ATOMIC ENERGY COMMISSION ---Page Break--- ---Page Break--- ‘TABLE OF CONTENTS I. Introduction II. Forest Ecology Isotope Cycling Studies 1 A Versatile Stemflow Collar for Interception Studies 7 Forest Recovery following Gamma Radiation 10 III. Animal Ecology Role of Amphibians in the Biology of the Puerto Rican Rain Forest 6 Classification and Geographic Distribution 16 Microhabitat 18 Reproductive Behavior 9 Vocal Organization 3 Evolutionary Relationships 32 Experiments in Niche Distributions and Energy Flow 38 Territoriality and Population Dynamics 38 Interspecific Territoriality 19 Feeding Behavior of the Frogs and Lizards in the Tropical Wet Forest 6 ‘The Ecology of Ants in the Luquillo Forest 6 ‘The Role of Insects in the Food Web of the Tropical Wet Forest 8 IV. Visiting Scientist Program Properties of Aquatic Communities in Container Habitats 8 Studies on the Chemistry of the Tropical Marine Atmosphere 9 Karyotypic Studies of Bats of the Family Phyllostomidae 9% Arrested Succession in Tropical Terrestrial Ecosystems 10 Field Studies on the Puerto Rican Tody, Todus mexicanus 109 The Termites at El Verde - 1969 Survey 10 Polyethism in Workers of Ischnoceranus costaricensis 10 Occurrence and Distribution of Aquatic Fungi in the El Verde Forest 229 Radiotracer Studies and Nutrient Cycling 10 ---Page Break--- “DETRoDUCtion ‘The Terrestrial Ecology Program is now in its seventh year. Approximately the first four years were devoted to studies on the effects of gamma radiation on a tropical forest ecosystem, Beginning in 1966,

emphasis was graciously shifted to the second objective; the measurement of Tali-cut mucLites in the rain forest system. This objective has since been modified to include the cycling of both radioactive and stable isotopes in the forest ecosystem; (1) fallout measurements; (2) tracer experiments; (3) stable element analyses; and (4) water balance measurements. In 2066, amount experiments using radioisotopes as expressed were begun in the tropical forest. The movement of "Ce, Bsr, Stn, Som in plants, animals and cell water have been studied and reported. Experimental work involving the movement of tritium in plant and soils has been successfully studied. Studies on the transfer of 3%, Stn, Tse and Fe from litter to soil and uptake by plants were completed this past year. Current research includes studies on insect ecology, movement of selected isotopes through the animal food web, element input via rainfall and its subsequent distribution in the forest, recovery in the irradiated area, movement and distributions of previously applied isotopes in the soil, plants and animals and Acoustical Communication and Population Biology in Eleutheroactylus species. Future work will be in the direction of the systematic study of the movement of selected radioisotopes in both the biotic and abiotic components of the forest. Increased emphasis will be placed on the physical and chemical properties of forest soils and the movement of macro and trace elements via soil water to the 'This report covers the studies that have been initiated or carried out this past year. Some are interim reports of ongoing research while others concern short-term studies that have been completed. The reports are grouped under three broad categories; (1) Forest ecology, (2) Animal ecology, and (3) Contributions from the Visiting Scientists Program ---Page Break--- FOREST ECOLOGY. Isotope Cycling Study, Clenents. Active research this past year has been primarily in the field of insect and amphibian ecology. Studies on radioactive and stable

Feotope movement. In trees, litter and soil have been inactive most of the year due to completion of

these studies during the first two months of 1969 and a change in staff. The results of these studies were summarized in the 1968 annual report (FRI-131); a more detailed discussion was presented by Jordan in the 1969 annual report of the Terrestrial Ecology Program (FRIC-129). The contamination of terrestrial systems with radionuclides may occur either by particulate fallout or via isotopes associated with rainfall. Foliar absorption of isotopes by plants is a fact. The factual uptake of isotopes from rainfall is a function of the intensity, duration, etc., size and the zenith of time the water is in contact with the absorbing surfaces. A review of rainfall distribution at El Verde from 1964 through May, 1966 showed that approximately 70 percent of the daily rain events were 0.5 inches or less (Table 1). Sufficient emphasis has never been placed on the importance of the small storm sizes and their role in the uptake of radionuclides. Fassig (1916) studied the duration, frequency, and intensity of tropical rains in Puerto Rico. He reported that, at the Caguas station, out of an annual frequency of 262 rain days, 160 rain days had rains between 0.01 and 9.10 inches. On the western end of the island, the highest frequency occurred between 0.20 and 0.39 inches; this data suggested that for the Inguillo area, approximately 69 percent of the rains were 0.5 inches or less. Ohm, et al. (1970) reported that light rains between 0.01 to 0.10 inches/hour accounted for 62 percent of the rains at El Verde. According to Libby (1956), cleansing of the atmosphere of particulate matter in a zone of precipitation is assumed to be fairly complete with 0.1 inch of rain. For context, foliar applications have been used to conduct nine clear instances in prune landscapes where better supplies of water can be absorbed. Studies on the absorption of radionuclides on the cuticle have indicated.

that the serenest uptake occurs at hours along Specification (ettsiphy 1960 aerator, and Wittwer, 1960). Bukovae and Wittwer (1960) also showed that the Sounts SF 32 'tuonsel acy with the seustare coniejges of the leaf surface. Witwer and Teubner (1959) have shown that “K, Fe, and ---Page Break--- Table 1 Distribution of rainfall by 0.1 inch classes for the period January 1961 - May 196, Recommulative Percentage Tercent of total Rain Table of Payments Class Store BEERS, ES5g QGASaeaRaaeesess PRS less than 0.1 & R &" 643 ‘Totals ---Page Break--- 32p and 355 can be absorbed by the bark of fruit trees and contribute to the nutrition of the underlying areas. Thus the deposition and subsequent absorption of rainwater by rainfall can be compared to foliar absorption. Considerable work has been done on rainfall and interception in the hardwood forests of the eastern United States. Helvey and Patric (2965) summarized what was available. They found it necessary to conduct their own experiments to estimate interception, since the use of that reported in the literature was restricted by sampling and/or methods of measurement. However, they did find that the published data on regression equations were fairly uniform. Re-analysis of these data led to the development of generalized equations for predicting the quantity of throughfall and stemflow from gross rainfall in eastern hardwood forests. The two equations were derived Y = 0.901P - 0.981 (n) S = 0.0bLP - 0.005 (n) where T and S are the amount of throughfall and stemflow, respectively, P is gross rainfall and n is the number of storms per season. Similar work in tropical areas is scarce. Mohr and Van Baren (2954) presented data on the amount of rainfall retained by the canopy in Surinam. They reported that with a rain of 0.04 inches, 604 was retained and this percentage decreased to 19.57 with a rain of 1.4 inches. Jordan (1968) initiated a series of studies on the water budget of the El Verte Forest. In this study stemflow was measured on 27 trees which ranged from

1.6 £0 30.7 inches DSH, Throughfall was collected using 12 trough type gauges located at various sites in the forest. We found streamflow to be almost a constant percentage of gross rainfall, ranging between 17.5 and 22.4 depending upon storm size. Throughfall was found to be approximately 70% of gross rainfall. Regression equations of the form ‘y = bx’ were developed for

each DBH class between 2 and 30 inches. It was found that intermediate size trees yielded the largest amounts of streamflow from a given storm. These equations were then combined with data on the number of trees per hectare and the DBH distribution of trees to estimate the contribution of streamflow to the water budget. In their discussion, Helvey and Patric (1965) brought forth two important points. First, a complete interception study has never been reported and second, streamflow has not been well documented on an areal basis. Traditionally, streamflow has been measured on individual trees and the results extrapolated to an area basis as represented by the work of Jorian (1969). Hydrologic studies quite often have been too restricted in scope and have not considered the full importance of the inter-relationships that occur on an areal basis. However, this approach has been restricted because of the lack of adequate techniques, especially in the area of streamflow measurements. Helvey and Patric (1965) pointed out that the paucity of streamflow data was no doubt due to the high cost and hard work involved in this type of study. Thus, if interception studies are to be initiated on an areal basis, the question of streamflow collars and measurements must be solved. We feel that the problem has been solved and the description of the streamflow collar and techniques is presented as a separate section. The objectives, methods and procedures of the comprehensive interception study are set forth in the following sections. Objectives: The interception study has four main objectives. First, to determine the quantitative relationships between

gross rainfall as measure! above the canopy and the parameters of throughfall and stemflow yield, litter interception and evaporation, and soil moisture changes. To determine the chemistry of each parameter and define the chemical changes that take place as rainfall is intercepted and redistributed as throughfall and stemflow. The elements to be determined are: calcium, potassium, soil, magnesium, manganese, iron, copper, zinc and lead. To develop predictive equations through correlation-regression analysis on the relationships between gross rainfall and the associated interception parameters which will include both quantity and chemistry. To utilize the information obtained for the design of future cycling studies at the watershed level using radiotracers. Procedure An 80m by 60m section of forest at the El Verde Forest site in close proximity to the 7 ft. walk-up tower was selected and subdivided into 36 smaller plots of 20m by 20m. Five plots were randomly selected for the studies. A grid of 1 square meter was laid down in each of the five plots and the location of each tree species, and its DBH were recorded. Notes were made for each tree regarding its bark characteristics, leaf size, presence or absence of epiphyte, and vines, and whether the tree was erect or inclined. Each tree was classified according to its interception potential as follows: 1. Primary interceptor - Those trees occupying a canopy position and receiving direct rainfall. 2. Secondary interceptor - Those trees occupying a sub-canopy position and receiving throughfall from a primary interceptor. 3. Tertiary interceptor - Those trees occupying a sub-sub canopy position and receiving throughfall from a secondary interceptor. One plot, from the five set aside, was randomly selected to initiate the interception studies. All trees in the plot having DBH of 3 inches or larger, 5 in total, were fitted with a stemflow collar (see section on collars). To measure throughfall, six troughs 6 inches wide by 2 feet long.

Vere fabricate! from galvanized metal. Each trough was lined with polyethylene sheeting. The troughs were given a 10 percent slope to facilitate rapid drainage of water. Throughfall will be collected in covered 20-gallon plastic containers and quantities determined by measuring with a calibrated click. The effective collecting area of the troughs is 13,696 in^2. Theoretically, one inch of throughfall would yield 34,709 ml of water, thus allowing the measurement of small quantities of throughfall. The troughs were selected over other means of gauging because of the interest in the chemistry of the water. In this way, the troughs integrate the throughfall and give a more

representative sample of the area than would spot sampling. Gross rainfall measurements are measured from a one square meter stainless steel collector located on top of a 72 ft tower. With an effective collecting surface of 10,000 in^2, a one inch rain would yield 25,400 ml, thus giving a sensitivity of 0.001 inch. Measurements will be made the morning following each rain and the data transferred to it for subsequent correlation-regression analysis. Samples will be collected from each rain for chemical analysis, which will be done by atomic absorption spectrophotometry. As the study proceeds, litter interception and evaporation loss studies will be incorporated into the program. Likewise, soil moisture blocks will be installed to monitor soil moisture conditions. Pressure membrane techniques will be used to determine the water holding capacity and drying cycles for soil layers down to a depth of inches. ---Page Break--- REFERENCES. Bidduph, O. 1960, Radioisotopes in plants: Foliar entry and distribution. Radioisotopes in the Biosphere. Ed. R.Z. Caldecott and L.A. Stryker. Printing Department, University of Minnesota. pp. 13-25. Bukovac, M.J. and Su, Wittwer, 1960. Absorption and distribution of foliar applied mineral nutrients as determined with radioisotopes, Plant Analysis and Fertilizer Problems. Ed. W. Feuther. Port Baltimore Press, pp.

215-230. Passig, Oliver L. 1916, Tropical rain - their duration, frequency and intensity. Monthly Weather Review, pp. 329-337. Jorian, C.F., 1968, The Rain Forest Annual Report. PRC-119. Helvey, J.O. and J.P. Patric, 1965. Canopy and Litter Interception of Rainfall by Hardwood of Eastern United States. Water Resources Research, Vol. 1, No. 2, pp. 193-206. Libby, W.F. 1956. Radioactive fallout and radioactive strontium, Set. 123: 657-660. Vohr, H.C.J., and F.A. Van Baren, 1954. Tropical Soils, Interscience Publishers, Inc., New York, pp. 27-99. Odum, J., G.8, Drew and J.R. Hine, 1970, Climate at 22 Degree. A Tropical Rain Forest. H.2, Out, Bl, pp. Besh?-M18, Wittwer, S.I., and F.O. Teubner, 1959, Foliar absorption of mineral nutrients. Annual Review of Plant Physiology 10! 13-32. ---Page Break--- A Versatile Stenflow Collar for Interception Studies

RG, Clements and José A. Colén one of the limiting factors in the design and initiation of large scale rainfall interception studies in forests has been the lack of an inexpensive, practical and rapidly assembled stenflow collar. Helvey and Patric (165) have suggested that the relative paucity of stenflow data was no doubt due to the high cost and hard work involved. This may explain the great diversity of collars used in previous studies and the reason why many investigators have dealt with individual trees rather than attempting studies on an areal basis. While the individualistic approach may provide an approximation of stenflow on an areal basis, this has two basic faults which are interrelated. First, and by far the most important, it excludes the interdependence on the influence of one tree on its nearest neighbor from consideration. Yet today, the ecosystem approach and systems analysis stress these interrelationships. To ignore these relationships leads to the second fault that considerable error may be introduced when the results from individual studies are extrapolated to an areal basis. Thus there is a need to revise the approach and begin studies for

an aerial barrier as suggested by Elvey and Patric (1965). The problem at the El Verde site centers around the cycling of both stable and radioactive isotopes in forest ecosystems. In planning the interception studies on an aerial basis, it was necessary to solve the problem of high cost and ease of installation of stemflow collars. This was further complicated by the requirements that the collars had to be made of relatively inert material so as not to affect the chemistry of the water collected. A literature search provided little if any help. After rejecting many concepts and suggestions because they did not meet the three criteria mentioned, a solution was found. The materials consist of two rubber sheeting one inch thick, 4 mil polyethylene plastic, rigid polyethylene tubing, contact cement, and refined paraffin. The foam rubber is cut into strips one inch wide, and the length depends on

the circumference of the tree. The two ends are coated with contact cement and allowed to dry. The second rubber strip is stretched around the tree and the two ends joined (Figure 1A). With a standard cork borer, a hole is cut on the drainage side of the collar. A rigid polyethylene tube is cut to the desired length and inserted into the collar (Figure 1B). This tubing may be heated and bent slightly and secures to the tree as shown in Figure 1C. ---Page Break --- Figure 1 Pictorial sequence of stemflow collar installation at El Verde ---Page Break --- Two inch strips are cut from 4 mil polyethylene sheeting. Contact cement is applied to the outside edge of the collar and one side of the polyethylene strip. When the contact cement has dried, the polyethylene strip is applied to the outside edge of the collar to form the trough (Figure 1C). Refined paraffin is melted in a glass beaker on a portable burner. The area surrounding the polyethylene tube is saturated with melted paraffin, which when cooled provides additional strength to the foam rubber-tube joint. The upper surface of the collar and the area between the collar and the tree receive

severe coats of paraffin to seal the surfaces (Figure 1D). The completed collar may then be connected to the collection container by the appropriate tubing (Figure 12). The plastic container shown has a 5-gallon capacity. We have found it necessary on some trees with high stemflow potential to insert a Y tube at the outlet of the collar and pass the stemflow water to two 5-gallon containers. The collars have been in field use for many years and show no signs of deterioration under the high rainfall and humidity conditions of the El Verde Forest. Repairs, if needed, are simple and rapid with melted paraffin. The actual cost of the collars is approximately $0.25 per tree exclusive of the collecting containers. The materials are inert and cause no problems with the chemistry. Installation is rapid. We estimate that 40 to 50 collars can be installed in a single day. References: Nelvey, J.O. and J.P. Patric, 1965. Canopy and Litter Interception of Rainfall by Hardwoods of Eastern United States. Water Resources Research, Vol. 1, No. 2, pp. 193-206. ---Page Break--- FOREST RECOVERY FOLLOWING GAMMA IRRADIATION George B. Drewry and Alejo Betrada A fourth annual census was made of all plants growing in a 476 m^2 sample plot inside the area of damage from a 1965 gamma irradiation. The census was completed during the months of August and September 1969, making results comparable to those of previous years. Mr. Jack Bvel provided valuable advice and assistance on field procedures. Data was processed according to general procedures outlined in the FY-1969 Rain Forest Annual Report (PRIC 129). Vegetation was separated by species within established categories listed in Table 1. As mentioned in previous reports, an arbitrary method of separating individual grasses was used, each species occurring within a square meter quadrat being scored as one individual. Extensive rootstocks in some species cause this method to overestimate the number of rootstocks actually present, with a consequent reduction in apparent diversity. Three

separate diversity indices were calculated for each category, as presented in Table ?, species per thousand individuals by the maximum likelihood method, average slope of the composite ratio curve, and Brillouin's index. ‘Composite ratio curves were constructed according to the methods described in TRNC 129. Additional experience with these indices has increased our understanding of their advantages and shortcomings. Brillouin's index, derived from information theory, is receiving wider usage among ecologists, although some persist in using the inappropriate (for biological diversity) Shannon formula. The principal shortcomings of the index are its relative insensitivity to interrelationships among the rarer species of a sample and its dependence on sample size. Species per thousand, obtained by any method, is complementary in that it is insensitive to gross differences in relative ratios of common species. In fact, counting the number of species in a random sample of 1000 individuals ignores all ratios. The maximum likelihood method of extrapolation ties the index to the ratios of the rare species taken as a group. It normally errs

slightly in predicting the exact number of species in a thousand, but errors appear random in either direction, and agreement in a large series of indices now calculated has been uniformly good. The composite ratio curve, which is the reciprocal of the relative abundance curve, can exhibit a variety of shapes, but its average slope in a semi-logarithmic plot achieves a compromise between the other two indices. It is less sensitive to sample size than ---Page Break--- Table 1. Plant composition of post-transplantation sample area (HT6 22) in summer 1969. Total individuals Species Radiation survivors Total plants Total trees Total new trees Total non-trees Tree seedlings Tree saplings Sprouts Total trees Vines Grasses Other Herbs Total Table 2. Diversities within selected plant categories by three different indices, summer 1969.

Species per 19% Average CK slope | Priziouin’s i pet Category Textsrapetates (species per tenfold) (bite per min.) ‘Tree seedlings 5a.c 28.2 Tree saplings Te 1.5 Sprouts: ue aE Oh trees role vines 56 Grasses 25 Other Herbs 12 Total New Vegetation Te 83.7 hos — a ---Page Break--- Briliouia's Hani veflests relationships in both rare and common species, with one exphasts on the rare. Breaks in the composite ratio curve are specific to certain vegetation types and have received special study. They are sharpest, and set off even in habitats that are most divergent from the areas, intensifying with indicate a ceo": would be winter. Figure 1, taken in conjunction with Tables 1 and 2, illustrates some of the properties of the diversity indices. The il parameter for both the vine category and the old trees is nearly the same, while species per thousand (x considerable extrapolation in the case of old trees) differ by a factor of more than 9. The staleness of the old tree complex probably affected it, for in two years since 1967, it declined by 205 with an average composite rate slope declined by only 185. At any rate, the diversity among the rare tree species is much greater than among the more common species, a phenomenon apparent in the composite ratio curve but not in the information theory index. ‘The composite maturity of vines does not exhibit a break, which lends to two hypotheses. The first is that vines are not strongly different from one another. This sweetens, partly supported by the fact that none show the same soil relative preferences that some tree species exhibit. A second hypothesis is that vines do not constitute any coherent community by themselves but are instead members of the tree or herbaceous communities, depending on their climbing habits. They all have a clear-cut specialization in common, relatively rapid growth without necessity for extensive lignification. This gives them a distinct niche yet makes them dependent on other plants. In overall diversity, according to the 1967 data, Figure 2 presents 1967 and 396. Macvepansies.

Involving the identification of grasses was severe! In the with Tron the 1960 senate. Pending Fecalculation, the 12H curve has been called and will be reported later. The similarity in vivacity and absolute ratio between 1967 and 1969 conveys very real changes in relative abundance between individual species. In particular, the decline of some shade-adapted species such as Dacryodes has seen novel into the abundant site of the composite ratio, (coplactne shade-adapted successional species). The only noticeable difference in the profiles is a slight increase in the diversity of the root colon species at the left of the curves. There was an increase of species from 7.3 to 7.7, and in a Prom bear to hear, we, the Ly date see very similarly Composite ratio curves for 1966, ---Page Break--- and 1969 7/1969 7 Old trees ranked order of abundance (species). Composite ratios of vines and the irradiated area, 1969 census Figure B ---Page Break--- Total New Vegetation Figure 2, Composite ratio irradiated area for 1966 ---Page Break--- Deaths among the cli trees surviving the irradiation accelerated somewhat during the fourth year, only 10 individuals representing 1 species remaining, compared with 66 of 42 species in 1967. Many of the post-irradiation sprouts, however, became established as part of the regrowth, and have become somewhat difficult to distinguish from the supplant category. One species, Sloanea berteriana,

poses no difficulty, as it has not yet lingered in the area, but is represented by vigorous vines that have followed the tree species in increasing numbers of individuals, species and diversity, the increase since 1967 being about 8% in each parameter. Leres, on the other hand, have decreased by about the same amount. Within the herb category, the ferns have all increased, serving to balance an even greater decline in most other herbaceous species. The irradiated area has continued to lag behind the mechanically defoliated control center in its recovery, at least partly because of shade.

cast by damaged but still foliated cold trees. Perhaps the most significant aspect of the relation is that unshielded plant tissues have been unable to recover, even by sprouting. Any trees that appear to be on the way to recovery by sprouting have failed, and the only individuals that have recovered in this way originated sprouts from below ground level or in rock shallows, etc. At present rates of removal, just a few more years should suffice to eliminate all of the above ground tissue exposed to radiation damage. The percentage of recovered plant tissue showing apparent genetic damage from irradiation has remained almost negligible. ---Page Break--- ANIMAL BIOLOGY ‘THE ROLE OF AMPHIBIANS IN THE ECOLOGY OF PUERTO RICAN RAINFOREST George B. Drewry ‘The rain forest surrounding PANC's El Verde Field Station supports abundant frog populations representing several species, most are native to Puerto Rico and are restricted either to the island or to the forest itself. Nomenclatural problems seem to have been largely worked out by such workers as Stejneger, Schmidt, Rivero, Grant, and Thomas. Ecological studies of one or more species have been made by Heatwole, Rivero, Majors, Turner, Gist, and others. This progress report describes a program to elucidate the role of frogs in the rain forest ecosystem and to describe the mechanisms by which species create and maintain separate specific roles. Ideally, such a study might document the patterns of distribution, speciation, and adaptation of all the species and reveal the dynamics of each at the systems analysis level, considering all interactions within and between species and the relationships to predators, prey, and other organisms. Specific progress has been achieved within such an ambitious framework by dividing the problem into phases and correlating earlier descriptive and qualitative information into a program of experiments that reveal the quantitative aspects of the relationships. Frequent benefits resulted from integrating this study with ongoing

research into other aspects of the rain forest ecosystem. For example, studies of radioisotope behavior have helped clarify the position of species in the animal food web structure. The use of radioactive tags now appears to be an ideal method of monitoring movements of individuals within the population and quantifying the effects of experimental manipulation. Phase T. Classification and geographic distribution. This phase was descriptive and qualitative; construction of a theoretical framework is almost complete. Of 19 Puerto Rican amphibian species mentioned or described in the literature, and subsequently supported by taxonomic opinion, a few can be eliminated because their geographic range does not contact the rain forest. The bullfrog, Rana catesbeiana Shaw and 9 unidentified species of frogs are recent introductions that have not yet been observed in the forest. The bullfrog is becoming common in freshwater lowland marshes, and the japia is reported by Dr. Manuel Vélez (personal communication) to frequent human dwellings in the vicinity of Isabela, PR. The native Puerto Rican toad, Bufo lemur (Cope), is nearly extinct, although Sarca-Diaz (1966) has reported a rediscovery in western Puerto Rico. Finally, the ranges of Eleutherodactylus cochranae Grant and E. cooki Grant have been examined by several workers; it appears that the former species is restricted to coastal plains, and that the latter is restricted to the Taniaras mountain range of southeastern Puerto Rico, which at present has no rain forest. These species are well-studied qualitatively but their quantitative ecology will receive less attention than the remaining

species. Bufo marinus (Linnaeus) is an introduced toad that has become very common in Puerto Rico, and its preferred microhabitat of bare earth, pavement, gravel, short grass, or cultivated fields makes it very compatible with the environment created there. It breeds in sluggish or still bodies of water covered to breed within the rain forest. It apparently penetrates the

forest along rosie or open trails to the tolerance x single individual can experience between breeding seasons, when adults return to water. From our observations, this penetration is limited to between 2 and 5 miles. ‘The remaining 12 species are all members of the family Heptodactylidae, a prominent family in the new world tropics, particularly in the Caribbean area. The current classification, which could change as a result of future studies, consists of Eleutherodactylus albilabris (Günther) and 11 Eleutherodactylus species. They are given elevation within the rainforest; they can be divided into forest and forest edge species by surveying the distribution of calling males. This distinction is obscure; somewhat changes in the habitat of most species with increasing elevation, which will be described under the heading of phase II, Leptodactylus albilabris, Eleutherodactylus cogatus, Tuomas, ', sntitensis: (hela and £, brittord family range over much of the island, while E. portoricensis, E. richmondi, E. heirok, E. green, E. vightnanae, Poked tt in Southeast, Bayling Family, . described in Grant and £."unicolor Ste,neser are restricted to montane forest. The distinction between E. portoricensis and H. cogatus was not recognized until the 1990 work of Thomas. This creates difficulties in interpreting the earlier work of Heatvole, Turner, Tist, Drewry and others who dealt with montane representatives of this complex. Both species are very common throughout the rainforest and later work to be described here fully supports the conclusions of Thomas. ‘The possibility exists that an additional montane species is still being confused with F. cogatus, but the weight of evidence so far indicates otherwise. aT ---Page Break--- Phase II - Microhabitat ‘The evidence for microhabitat preference, like that for distribution, has been derived from the literature and from personal observation on numerous field trips, and is more qualitative than quantitative at this stage. Most of the conclusions rest on

agreement of the animal's morphology with the data on where a species was common, where it was rare, and where it was not found after reasonable search. Some modifications are still being introduced, but the major patterns seem to be established. The most relevant aspect of morphology pertaining to microhabitat is probably the ratio of toe pad diameter to body weight, which appears to reflect the importance of vertical surfaces in the animal's way of life. This ratio is lowest in Richmond and V. vishwanath, whose females were collected at ground level. Males of the two species often climb to low perches on vegetation while calling, but even then a horizontal perch is normally selected. The highest ratios are obtained in I. cooki, B. warlachmctt, E. hedrickti, and E. soquats. Both sexes of the first two species frequent the surfaces of boulders, while the last two are arboreal in tall plants and both have been collected as high as 40 ft above the ground. The walls of buildings are also used by E. cout and it is the only species commonly encountered in this microhabitat. Eggs of three of these species have been found attached to the underside of horizontal surfaces, which indicates climbing ability, while B. warlachmctt frequents inaccessible crevices between stream boulders (the eggs have not yet been observed). The pad diameters of the remaining species range between these extremes and correlate well with observed behavior. Other, more subtle correlations between microhabitat and morphology probably exist. For example, the color and texture of the skin may relate to the favored positions of daytime concealment. Another possible correlation is the fact that in rock-dwelling species mentioned, the eyes are larger in relation to body length than in species arboreal on low vegetation such as E. scintillens and E. beittont, which may detect prey as much by vibration and touch as by sight. Evidence that different features of the microhabitat are used for orientation by different species can be deduced from the

varying behavior of species with altitude. Four vegetation zones have been derived for the Luquillo forest, with each bearing the name of the dominant species. Beginning at the highest elevation, they are the mossy forest, the palm forest, the colorado (Cyrilla racemiflora) forest, and the tabonuco (Dacryodes excelsa) forest. At certain localities in the palm forest, one can encounter most of the frog species within a very short distance, although microhabitat segregation is noticeable even here. If one moves upward into the mossy forest, first E. beittoni, then E. aubluensis, drop out of the fauna and E. hedricki becomes rare, while most of the other species become more abundant. In moving downward, the segregation is more pronounced; E. helgicki and E. portoricensis become more and more restricted to deep shale and less common at the forest edge. By contrast, E. antillensis and E. pritenti are absent from the forest proper at lower altitudes, and Z. locustus and I. gryllus become restricted to the forest edge, often appearing either in deep shale or surrounding grass. Grass is restricted to the very high elevations. It makes contact with the soil and represents where the loose but water-saturated and receptacle soils typical of mossy forest give way to finer, slightly more compacted and often oxidized soils below 700 meters elevation. The other species range to the forest edge at all elevations. ‘Table 1 summarizes the microhabitat preferences noted for each species. Where behavior varies, any bias is probably toward the conditions in the vicinity of El Verde Field Station, where a large fraction of the observations have been made. Elevation of the station is 1,500 meters. The table is organized in approximate agreement with the phylogenetic evidence presented later (Phase IV). Phase III. Reproductive Behavior The third aspect of the natural history studied in the initial descriptive survey was reproductive biology. Reproduction in Bufo has been mentioned earlier and is well described in the literature, but the long-

breeding migrations apparently made by B. mactans from the rainforest. reserve within study. Jeptotactylus albiscens breeds in the typical manner for its genus, with pairs constructing four nests in burrows or natural cavities under banks and stones in many areas near shallow streams. Males call from such shelters and are seldom encountered far from water. However, both juveniles and females forage for long distances into nests and on the forest floor. The eggs hatch into tadpoles which either grow into large aquatic larvae (when water and food are plentiful) or metamorphose at a small size into terrestrial froglets (if conditions are dry). This pattern of development seems to represent an intermediate stage in the evolution of the unique condition found in the next genus, Eleutherodactylus, one of the few amphibian genera that produces completely terrestrial eggs. The entomology was first described by Peters in 1871 for 2 Puerto Rican species (probably E. coqui). The tadpole stage is passed within the eggshell and at 29 ---Page Break --- ufo martins 2000 nar, leo: 3000 aa. Seema ain, micclor 2000 min, acclimatats 400 ats, coat too ain. ut vee persistence 300 min, jautibiensts 3009 max, peistont 2500 ms wingmass 00 ats, edge 900 ata. 900 ai. courts 590 ain. 300 mae. 500 possibly extinct most of Latent cuaters mountain forest southeastern mountains most of overall plain wear of dwellings leis, anima, roate ales malty areas, female orange taely se grown a mies sata dwellings roseut shrubs, palms, hexbe shrubs, seeds in sun areas forest floor, especially Teter Nee luuaiy limits to tree holes ots covered ulcers and atansnente openings and edge of forest, Hrctaiay fem thickets and marshes, wet network, Lawn penis and edge of torrent ev canopies tee branching northeastern coastal plain swamps and ponds ---Page Break --- hatching the young are fully metamorphosed froglets with reabsorbed tails and functional limbs. Several writers have mentioned that a parent remains near the eggs during development, this has been in

Correctly assumes to be the female. In the course of this survey, the eggs of E. cook, 5. hedrtoxt

and £, cogui have been observed, the latter two having been seen repeatedly in the course of development followed. In all three, the eggs have been attended to by the male parent; in the latter two, the eggs were attached to a wall of ‘the shelter known to be routinely occupied during the day by that male. When in the shelter and not disturbed by the observer, he kept some part of his body in contact with the egg mass, usually the lateral or ventral surface of the abdomen. If disturbed, he quickly left the shelter and hid nearby, but returned within a half hour or 30 minutes to take up the same position. Eggs were observed to increase in diameter during development, even when the shelter walls were tight, indicating that water was absorbed from the skin of the male. Males were seen to travel at night to nearby sources of water where they drank by the usual amphibian method of skin absorption. Thus, in the species observed, such parental behavior is probably essential to normal development; in two cases where males were removed, the eggs failed to hatch, hatching requiring approximately three weeks. The young remained in the shelter for about three days, sitting under or in contact with the male or with the collapsed egg skins, which remained most. At the end of this time, the young dispersed immediately, day or night, if disturbed; but undisturbed dispersal occurred at night and was not observed. Egg skins and remaining undeveloped eggs disappeared within a day after dispersal of the young; the exact method of removal has not been observed. The species most thoroughly studied has been E. hedrtoxt. Although rare by comparison with the rest of the species, adults of both sexes occupy tree holes, many of which are near eye level and are open enough for easy observation. Although, to our knowledge, no one has actually observed copulation in Eleutherocactylus, Clayton Glot (personal communication) was able to bracket its occurrence closely by.

routinely observing for several nights a group of males whose shelters were known. He reports that a female was observed at 2100 hours in the shelter of 1 male known to have a week-old egg mass already developing. The pair were not in amplexus at that time, but by 0900 the following morning a new egg mass had been placed in contact with the old one. The female spent the day within the male's shelter, departing between observations at 1700 and 2100 the second evening. Males of this species continue to call from within and near the shelter while they attend eggs, and have been observed to accumulate as many as three egg masses of different stages of development. ---Page Break--- Occasional observations of incubation by Coquille are facilitated by their habit of adopting human artifacts, such as flowerpots, glass or metal cans, and cardboard boxes as shelters. In the forest, detritus-piles and axils of plant stems seem to be the most common shelters. Numerous Coquille nests observed have always consisted of a single developmental stage. One male observed periodically throughout the course of four successive broods did not call while incubating except for a few occasions when new males began calling in his vicinity. At these times he emerged quickly from the shelter and called strongly until the newcomer stopped. Additional observations regarding this species are reported under the heading of phase VII. Bag care by E. Cook was observed once, and comparison with the observations of Duan Rivero (personal communication) indicates that it is typical. A male (verified by catching individual and observing vocal pouch development) covered with his body an egg mass attached in a shallow concavity on the underside of a large boulder some distance below the ground surface in a boulder grotto. When released, he hid in a crevice but was seen about an hour later on the eggs. He did not call during the time watched although other males were calling at distances of about 10 feet. It is not known whether the site was a spot

habitually frequented by the male. Clearly these scattered observations need to be supplemented. ‘The slow accumulation of data is due largely to the diffuse nature of terrestrial breeding, when compared to the large, usually seasonal aggregations of water-breeding terrestrial frogs. most

Eleutherodactylus leave their shelters secretly and rapidly in the evening, and enter at dawn; territory-holding males seem to utilize the best concealed shelters available. The weight of authority stating that females are the attending parent (Schaist, 1928) is an additional problem. Heatwole assessed (personal communication) that a clutch of, richmondi eggs discovered in decaying logs were attended by the male, and did not attempt to determine the sex. An entirely new set of hypotheses about the reproductive dynamics of Eleutherodactylus requires consideration of the terrestrial breeding pattern, the demonstrated male territoriality, and the implication of male attendance (regarding the only three species unequivocally studied). When males hold reproductive territory they increase the probability that their own genetic line will be propagated by mating with the nearby females; they also reduce the contribution of surplus males by suppressing their reproductive activity or forcing them to set up territories in marginal habitats. This appears to be the situation in E. hedricki, whose populations may be extrinsically limited by the availability of suitable treeholes and the ability of the very young to reach treeholes in the arboreal habitat of this species. ---Page Break--- The young of E. coqui, however, seek shelter on or near the ground, and only large juveniles and adults are strongly arboreal. The apparent refusal of male coqui to accept new mates while attending eggs, combined with continued defense of the existing territory, could therefore serve as an intrinsic, density-dependent mechanism for population limitation, forcing surplus reproductives of both sexes into marginal habitat, and keeping the territory free of.

Sonpetitive youns at their voow nirersus, least acbize ace. The following observations may be relevant to the hypothesis: (e) the populations of normal frogs prelatezs such as emill nawnale and Snailes are unusually low in Puerto Rico; (b) free populations of many species are extremely high; (c) vocal activity of frogs in Puerto Rico is greater than even the population densities would lead one to expect; (1) the vocal activity of males produced by some species indicates that vocal functions other than simple mate attraction are being met. A hypothesis receiving some attention from ecologists recently is that overlap in ecological niche between territorial species can favor the development of interspecific territorial behavior. Ortans and Horn (1904) and Orians and Willson (1964) clearly outline this hypothesis, and their studies of blackbirds with partially overlapping zones support the theory. They considered the view that defense of feeding territory from which the young were supported by the adults, and stated that the structural complexity of the habitat controlled the energetic expense of defense through the amount of patrol required; most habitats are relatively transparent to count, however, relatively inexpensive modifications of acoustic territorial signals should enable them to carry interspecific messages. The learned mimicry of such bird species as the mockingbird probably functions in this realm, and much other mimicry may be uncovered by experiments that elucidate the exact nature of territorial, distinguished from mate attraction, aspects of the calls. The converse of the above hypothesis could even be true in forms as strongly acoustic in orientation as frogs; that the demonstrable function of interspecific territoriality mediates the amount of potential niche overlap between the beneficiaries, normally the young. Phase IV - Vocal Organization A survey of vocalizations was made in collaboration with Dr. A.S. Rand of the Smithsonian Tropical Research Institute. Calls were tape recorded, using several

recorders at different times. Segments of activity 2.4 seconds in duration were analyzed with the Kay Electric Sound Spectrograph; one or more calls for most species can be included in a sample of this length. The frequency composition of each call and of whole assemblages were analyzed both with the sound spectrograph and with a Ba K type 2107 Frequency Analyzer. Vocal organization over longer time intervals has been sampled from tapes and outdoor microphones using the analyzer, a diode demodulator and a galvanometric chart recorder. Early efforts to continuously monitor selected species with Pixel cord filters tuned to dominant frequencies have

yielded equivocal results because the species were discovered to shift dominant frequencies in the course of the year. A scanning and integrating system which will cover any desired portion of the audio spectrum in approximately one hour and continuously record a series of spectrum plots is currently being placed in operation. All but a few overlapping species can be picked out as separate peaks in each scan. These have differing activity cycles, so their periods of peak activity appear distinctly in time. Figure 1 presents sound spectrograms of representative calls for each species; these are tracings from which background sounds not produced by the individual frog have been edited. Compression and mark levels of the machine were adjusted to print only components that were within 12 dB of the loudest component. Although weaker components are frequently useful for deducing attributes of the sound-producing apparatus, they have seldom been found to have biological significance. The calls presented in Figure 2 are considered not to be functionally homologous to the regular calls and their functions will be discussed later. Figure 3 presents vocal organization over longer periods of time for those species which have been adequately studied. Resolution on this scale is not always enough to show individual notes, and some calls composed of rapid

Sequences of notes are shown as single marks. Another compromise adopted in this presentation is the selection of a vertical scale; an attempt is made to simulate oscilloscope format, where mark width is equivalent to amplitude, but where notes represent different frequencies, as in the case of E. corythaeola, the wider marks denote the higher frequency. Mark width denotes duration in the case of E. enetase, 3. locustus, etc. A working vocabulary has been developed for the verbal description of vocal parameters; it agrees in general with the usage of other bio-acoustical workers, but differs in slight details. The note, taken as the basic descriptive unit, represents the sound modulation produced by a single contraction of the thoracic musculature. Notes can usually be identified by observing the body wall and/or vocal pouch of a calling animal. In recorded sounds, notes can often be identified by observing the wave-form envelope on an oscilloscope. Because muscles cannot reach full tension instantaneously, the leading edges of notes are rounded, with a relatively gradual rise-time in intensity (note the exception below). ---Page Break--- arteeee reese ---Page Break--- aoa TRETTS one - ow & HO he SS uy ur bass ---Page Break--- Figure 3. Calling patterns of ten species of Puerto Rican Eleutherodactylus. See text for additional explanation. ---Page Break--- Many species use structures within the larynx or the glottis to introduce pulse modulation within the period of single notes (Martin 1967). The repetition rate of these pulses can reach an appreciable fraction of the vocal chord vibration rate. In some species the vocal chords themselves produce low frequency pulses which may or may not be further modulated by other structures; only the higher harmonics of the pulses are coupled to the air from the radiating surfaces of the vocal pouch or body wall. In other species the vocal chords vibrate at high frequency and only the incidental lower harmonic is coupled out, providing clear whistles or

peeps. Low Frequency pulse modulation is always audible as a harsh grating or squeaking quality in the sounds it is identifiable in spectrograms as sharp vis-a-vis pulses and in sonar echoes as a series of spaced lines whose spacing defines the pulse frequency. High frequency vocal short vibrations with secondary pulse modulation appears in sonograms as a central, strongly dominant frequency with more or less symmetrical sidebands above and below, while pulse modulation by the vocal chords themselves appears as more smoothly spaced harmonics whose amplitude distribution outlines the response characteristics of resonant structures in the acoustic pathway. Pulse modulation is evident in the calls of E. richmondi, E. karlschmidt! and unicolor shown in figure 1. Their general relationship to one another is discussed later. Low frequency pulse modulation is a potent source of confusion in discovering acoustic bounces, as low pulses are analogous to plot

note repetition rates, considerable overlap occurs in arena anew whole. Confusion is normally resolved by observation of calling animals. Frequency changes in successive pulses of sound often indicate that the animal is holding continuous muscle tension, while with each pulse vibrations travel from the system to the vocal pouch or mouth, changing the resonant frequency of these structures. A final confusion arises from the possibility that the pulse forming structures take close between notes, opening explosively at the beginning of each note to confer a fast rise time and produce a wide band noise to be shaped by the filtering action of resonant structures. The clicks of Gryllus and the longer notes of Beliri are believed to result from such action; the beginning tends to produce a vocal bandwidth that lacks distinguishable sidebands and appears to be a filtered noise, while the remainder of the note resembles the w pulsed introductory whistles. Thus, each click is a single pulse it is also a single note as suggested by the lack of progressive change in dominant frequency.

went easily verifiable by observation. The clicks of E. suyilue exhibit a trend, however, toward pulse-modulation similar to that of S. riebmonal. The pulse forming structures apparently vibrate through the course of the note and superimpose pulse modulation ranging from slight to fully developed. The changing dominant frequencies of E. cogu, E. portoricensis, and E. antillensis represent more sophisticated vocal artistry than the passive shifts that occur as a by-product of low frequency pulse modulation. These are two-note calls, as verified by observation of the body wall, in which vocal pouch resonance is changed by moving air in or out in synchrony with the laryngeal mechanisms, in a manner analogous to the playing of a trombone. A more exact idea of the precision involved is gained from imagining a hybrid instrument between a trombone and a single key accordion; the air volume of the instrument controls the resonant frequency and at the same time the air movement powers the reed. Thus, the reed must be keyed in and out at the exact times when the charging volume is right for the notes to be played. Individuals of these species are sometimes observed to miss the exact synchronization required and produce weak, off-key notes. They also engage in tune-up procedures reminiscent of human musicians. Calls represent the next level of organization beyond notes, and the calls of several frog species consist of single notes. The unit of repetition defines calls where repetitive sequences of similar notes occur, at least if the differences involve frequency or note duration. The difficulty in interpreting the present species occurs with E. beittoni, which produces sequential clusters of increasing numbers of notes. The number of notes at any given point in the sequence cannot be predicted exactly, however, which suggests that each cluster of notes is a separate call. The hypothesis is strengthened by the similarity to the call organization of E. gutillensis in figure 2; other evidence for their

Close relationships are given inter. The notes of E. hedricki are harder to interpret; they may be one note or a sequence of notes. A later discussion of relationships suggests the latter. Despite the rapid note repetition rate of Leptodactylus albilabris, the unpredictability of note number indicates that each note is a single call. There is no sign of note organization in that species; an unvarying sequence of notes can extend for more than an hour. The term “call group” applies to a series of calls separated from later, similar series by periods of silence. In those species exhibiting call groups, the number of calls per group cannot be predicted exactly. However, call rate does characterize each species and is the basis for discovering the distinction between E. coqui and E. portoricensis (Thonas 1966). The function of call groups themselves will be discussed more fully in phase VII, but it was noted in the survey phases that the beginning and end of the daily cycle of vocal activity involve periods of continuous calling in which call group organization is not apparent. At these times, males are apt to call from within, or very near to, their daytime shelters, where the range in those species observed are reported. The implication is that mate attraction may occur

during these periods, leaving call group organization to be a territorial device. The hypothesis is strengthened by the fact that, as call group organization develops, the males climb vertical structures, sometimes high above their daytime shelters. ---Page Break--- Available data on the organization of vocal activity in the animal cycle is diagrammed in figure 4. This preliminary information is pertinent to the quantification of animal changes and a better understanding of climatic and situational variables. As stated in the section on microhabitat, the species do not respond to the same variables in the same way. For example, the vocal activity of E. coqui seems to be more influenced by humidity than by temperature, while the reverse seems to be true.

F. hedricet. Although both call actively cn vari, vet nights, only E. hedriekt Je very active on warm dry nights, typical cv in late March and early April; occasional cool, wet nights in the same period reverse the relative activity. Most of the species appear to be stimulated into activity by sound, including that of other species. The only one that appears to be negatively affected by other species is E. karlachaidti, which gives the subjective impression of "lingering silences," even at times during the day. This species and E. wightmanse synchronize calls closely with other conspecific males, and seem to be stimulated to call by flashes of light from passing automobiles, etc. Many of the species respond with calls to the onset of showers, even during the day. Heavy rain can depress calling activity in the smaller species such as Z. Drictont and E. wightuanses; perhaps the mechanical effects of striking raindrops are responsible. Not enough data is available to compare annual patterns in vocal activity. B. richmonl! appears to be stimulated by low temperatures; it is maximally active on the coolest nights while most other species, except possibly S. kurlechm!, and the inadequately studied E. unfcolor, are silent. Again, the slope of correlation with most of the affecting weather variables differs between species. The Rain Forest Program Annual Report 1964 stated that temperature and humidity alone were inadequate to account for seasonal changes in the vocal activity of the E. portoricensis complex; hormonal changes are believed to be involved. The frequencies monitored in that study, incidentally, lie in the band of overlap between the second notes of E. cogut and 3. portoricensie, and activity levels of both species were actually stilted. Appendix 1 provides a key to the vocalizations of common Puerto Rican frogs; only the ‘ylg and Bufo lemur were not studied in our survey of vocalizations and are omitted. An effort was made to make the key usable by non-specialists; terminology not found in standard dictionaries.

avol ‘el ani no measurements are required. ‘A tape of typical calls of each species has also been prepared- ---Page Break--- mie mim mmm ---Page Break--- Phase V- Evolutionary Relationships ‘The survey also tried to establish the main features of evolution in the Puerto Rican Eleutherodactylus; the dynamic equilibrium, which is the real subject matter of ecology, can be most profitably interpreted when it is considered over an extended ‘time, and, conversely, evolutionary trends are most meaningful in the ecological context. A tentative pattern of relationships can be derived from the information in Table 2, which draws on morphological evidence, chromosomal studies, and the patterns of vocal organization. Comparative morphology of Eleutherodactylus can be seen in Appendix 4H, which is a guide compiled from our experience in field identification of species, and is also intended for use by non-specialists. Numerous errors are probably still present, and additions, corrections, or suggestions will be welcomed. The toads (Bufo), the bullfrog (Rana catesbeiana) and Leptodactylus albibrachius are not included; their identification should pose little problem, since all of them lack expanded toe pads, the bullfrog has webbed hind feet and the toads have dry, warty skin. Differences in size of eyes and toe pads of Eleutherodactylus received considerable attention from early classifiers, but are not reflected in the patterns of relationship outlined in Table 2. The results from application of the theory that features

of the greatest ecological importance are now rigorously subjected to the action of natural selection, i.e., structures and behavior used in foraging, concealment, reproduction, and locomotion within the microhabitats, thus, they should tend to change most rapidly in evolutionary time, whether the changes are parallel, divergent or convergent. The vocalizations used to attract mates are particularly subject to pressures toward divergence, since failure to achieve recognizability can only result in the production.

of Wybrids, which are apt to be non-viable, stevie or otherwise poorly adapted. The morphological features of color and pattern have long misled the prospective student of Eleutherodactylid classification; some of the species, including the common soqul, sustain a system of color polymorphism that fascinates geneticists, but only confuses the effort to identify species. If the indicated relationships are correct, polymorphism itself is partially interdependent on phylogenetic proximity, the most extreme species apparently being Chromosome number is perhaps the most fundamental characteristic selected for inclusion in Table 2. This characteristic is relatively conservative, since it is not subject to strong selective pressures. Only two numbers appear in the Puerto Rican Eleutherodactylus fauna, 2N of 30 and 26, and neither the numbers nor the number of chromosomes ---Page Break--- Table 2. Tentative pattern of evolutionary relationships in Puerto Rican Eleutherodactylus. rt term hour synchro- glass E. rhodomonat 30 P - w . imieoior 2 E. keriscimtitt = 30 Pe 2 B, coqut Boor: portaricensis antillense a 26 2: w: 2G R: 3: abbreviations nse Po prominent and steaight R Younle! and curvel feat to back Ho intervenes ay present. Ly absent Inategiately 00 e 3 ---Page Break--- ams based on centromere location indicate that one may have recently derived from the other. Chromosome morphology is being studied in collaboration with Dr. James Jogart of the University of Texas, who has evaluated the chromosomes of several Central and South American Eleutherodactylus species. He has not found the 26 number there and though the evaluation is not completed, it appears that the 26 chromosome species from Puerto Rico are fairly consistent internally and not closely related to any other species in his study. Chromosome numbers of species on other islands have not yet been determined; the 26 number or derivatives from it may be associated with the suriculatus species group mentioned by several authors, with representatives in the Caribbean.

islamic. If so, this group might be elevated to the status of separate remus. Chromosome morphology between those species in Puerto Rico having 30 chromosomes is not particularly consistent and the next other differences suggest that they have had long independent histories. ALL however, has the pulse modulation in the call, and tend to be more active in cooler weather than the other species; they also have a straight, fairly prominent canthus rostralis, and almost no color polymorphism. The species having 30 chromosomes can be subdivided into two groups based on the shape of the canthus rostralis and the tendency to organize calls into call groups of progressively increasing call rate. The status of . wishinense is uncertain, and may occupy an uncertain position; it has two frequencies (Figure 1), that exhibit call group organization (Figure 3), and its call rate does not tend to increase within call groups. Call rate increase, termed “ramping,” distinguishes five species; 2. could represent closely the ancestral morphology and vocal organization. Three of the ramping species have regular two-note calls of obvious morphology (Figure 2), not ceweiona. as le (Figure 2), with a slightly higher pitch and multiple notes that show morphology to the regular calls of the other two species. The calls of E. brittoni are complex, increasing in both the number and rate of notes, but are probably derived from an ancestral pattern common to that of B. antillensis. These two species are very similar in morphology and habitat, and possibly diverged only slightly longer ago than E. coqui and E. porto- Picensis, which are the most similar species pair in the fauna. It is noteworthy that E. yowtoricensis places less emphasis than

species E. coqui on the higher pitched note in its call, and could be in the toning tea process. Not enough data is yet available to assure that non-ramping species constitute a coherent subgroup. To some extent, vocal organization characteristics cut across patterns of maximum morphological.

sinflartty, There Lo a clear link detween E- iosustg apa E. cochrane, vfeli has been discussed by Slvere ant Majcrea (1963) 3h ---Page Break--- ‘The sane pattern of call cryantzation and structure te shown by E. gpeiine, te. no call groupe nn a whistled Lone note followe’ Ey a Series of clidis, vith ittie tentency to tlgnt call synchronization between neigtoors, Dut the latter species also has norphclcsicai affintttes ¥ith Z heizickt. The notes of 2. heartoxs coul: be interpreted ao lenztiene? citcks, sinus an Introductory vhistle. In that Interpretation s whole sequence of notes woul? constituse @ sinsle call, Each sequence Lo normally given in eynehrony vith Feighboring Iniividuste. ‘The gynchrontzation of B, vightmanne !6 clearly et the call, rather than the call croup level, with larse munbers of inifviduale calling almost as a single frog. The cals of E. guyllus, on the other bani, seen to be synchronized at the cail group level. Their orguatzation sens to be einilar to, tut slover than, thet or E, brittont. The etuly of E, pryllus has been jumperes ty'the eisrioulty oF placing a microphone 90 that caliz of one inliviiual are distinguiehable fron others, At the elevation of the E2 Vere Etation, the species usually calle highin trees, ant calling males appear'to be clustere’ in the cane or adjacent trees, with noncalling indtviduass frequently encountere! far fron the chorus. This 1s the only species where the males show any evidence Of congregation. ‘Thecozest norpholoyical affinities of the species seen to be with E, Leoustus. ‘The curvey of relationships will, hopefwlly, be stvensthened by 4 survey of bicchewical sintlarities, using modern techniques of chronatograpty ani electrophoresis, Chenissl characteristics proba bly have a whole epectrum cf sensitivity to selective forces, and Will need to be evaluntei in canjunction vith the otter cats. An effort vill aloo Le male te inteneat students of comparative cote- ology in the opportunities presented by a genus in aueh an apparently active stage of species

fornasicn. he piylovenetic “versences and cenversences in the frog fauna of Puerto Rico will ve sicnificant in the brouier interpretation of the evolution of rperies Ivevsity in the tropics. Taland faunas have slreviy contribute! uniquely In this eapeat, beccuae the ever present problene of {sland dtcpersel have filled a vartety of ecolorical niches Sith closely related species, in which evolutionary trenle ure nore eaclly Uscernec. The contribation of the finches of the Galapagos Islanis to the evolutionary theories of Charles Darvin is @ elxseic Lllnetration, Poise VI - ixperinents in Hiche Definition and Enerey Flow ‘This and the vemintns phase of the study are still in active stages oF data collection an} will depend on quantitative results lant experimental procedures to test Aypotheues already outlinel, to 35 ---Page Break--- genernte nev cnes, ani to round out our understanding of the e00- Logical roles playe! by frogs. A detaile! stuly 1s nov being con- omoted on the types of prey items found in the stomachs of each available forest *ror species; a progress veport is presented under a separate healins. Frogs in the vicinity of all experiments] eftes Involving guma-enitting raliofaotopes have beon monitore! for uptake. Since {nitvidual frogs ter to rensin for long yertols of tine in’ one area, repeated weasurenents 0° the cane Iniividual have been obtained. Aninals were capturel, vhole body Live-countel for gama radiation, marked by toe elipping if not previously marked, ani released at the point of capture, Swwples have Veen small, out encugh asta hac been aeoumlated in three experinents Lor preLininary conclusions to be reported ant much infermation relating to esign of future experinents thas been gathered. In one experinent, 4c, sr, hin vere applied to & square meter 2 ee ee neh eer etre aU fo, eee eee ee ee ee eee ate Troga of the E. portoricensig complex (not separated then) ami 3 See a cee aoe ere ee Cae acscon of 13h4es approaching those in the plants reoted in the plots; isotope SESSA TOE Le ne

ate a ee en ee oo ar tia sues retaine? Lhe, (it was generally distributed in the body), but Pieireaietan feed pep mer enp reenter ShgY BS ESSE SESSA ae Se her ection a tse tit Siete Te 2) fos amir of Egagus ewes swore pets of SS Ina secon experivent the eptplytic bryostyteg, 2tchens and algae associate! with tree crus vere labelled with Obzn, ‘Three trees ore use! uni the coist‘on wis appliel to the first aix feet of eaeh tuk, Four spesinens o* E, sequl ani one of Z. Bedeioel, monitored over & two year pevic!, sextet equil brim consertration rangise Fron avout 199 ope per sam above bichgrcunl for a frog resident on ne of the trunk to 29 ey per stim in a S705 iiving ? meters axa gna different trust, Sever. inisviduale of the terrestrial species E, Hetmonit ant £. dightwanse faile! to shew seasumnble uptate. Ulearas stow! wish Bicker levela of uptnre tut none of the predatory yertedrater approarhe> the levels reached ty snails of the genie Sarncollus after even a single nivht of foraging on the trunks, Tt ia conciasea that the verteirates iil nov ‘getty or gerhape Atgent, the labelled plant material rectly ant probably’ recetved thet intake of dsotepes via prey that hai fei dineotiy or tndtrectly on the plants. 36 ---Page Break--- ‘he thiri experiment Is sluost negative so far as ‘sotone uptake ly Tregs 19 fonceme!, but the methoiy developed show poise for future etuttes. tare cuncpy trees were inJectes with gama- emitting iectepec In two stuiy plota about 60 meters apart. caf- fold towers alacent to the trees sere erected beforehani, ani in aan effort to inereace frog populations in the areas, 28 nodes of ance vere attaches ct 1/? Tost Intervals to each of txo dlagonal= ly opposite tover 1egs. “The n-‘es were out sc as to be closed at Doth enis with a nctst Joorvay near the bottom end. In four monthe ‘the lover 22 shelters (38 1/° feet) on ench tcver vere colonize ty. E. cogut api £. petriski of both sexes, lth populations stabilizing St Shout b melee ant % to & fevslea on each tover, The tree besides one tover

was tagged vgth Sgr. At thy other site one tree vat tog~ ged vith « mixture or €35r, Sr ani Syn; = second tree vas labeled vith Ufes. “detalls of thece experiuents arg siven in the Rain Forest Annual Report 1969. APter 18 sonthe Sr ant Tce are the only Isotopes detectebie in the tree leaves. Canopy foragin: Lizards of tvo ypectes in both sreas show: measurable uptake of Sr ty the fall of 196) but ground-svelling specter it not. ‘The tover frog populations have Veen gewsa-counte at intesyals of atout two nenthe. In Februsy 1070 a single Texte 3, cogul Living near the ground showed a Darely nessuratie (less Than 10 cym) uptake of ico, after having Deen nezetive in ece. At that tine, 2tter-tvel-ing frogs vere tested fer !37es. ‘wightrsme had reasurable Levels, while two juveniles E, not. Tost of the tover population cf rrogz renwin wiiccntauinated ty either iectope, a2 do the round vel rie. Future tracer experinents to stuly energy flow appear pronting ani can provide “uta on both the Tate of rwitemietises Intreauce! in the systen and the sources cf enery tappe by various Branches of the shina? food veb. A proyosed experizent veulA Iabel living plant Same with one isotope wn. the Jeccnposine compartment vith a second Asctore. mntnent wuli uge the vane isotope pair in reverse seniteslar the gradual mixing of these iectopee ani in the Litter layers, a source ratio soul! te developed with vhich 2 ovapare ratios inthe predatory aninals. Ratios Ln these snlvale might then provile an estinate of the relative proportion of pey thut are herbivores ani saproverea, ‘ani tins quantity the tr-ctich of energy passing throueh the plant Gecemporer congartzent before entering the wsiimsi Tool veb. This fraction is expecte! to be hivh In the forest generally, altheugh Digher for the prevstors tvelling in the lister layer than in the arboreal epecies. Dini lar eyperinenta sing ratio: of paized Leotopes in reciprocal applivaticns (a2 a control on differences in Lootopes Behavior) can be use! to compare energy flows fren decomposing

fruits and leaves, leaves on stems, or many other combinations of ecosystem components. All of these would supplement insect analysis of stomach contents in defining differences in feeding niche. ---Page Break--- Phase VII ~ Territoriality and Population Dynamics Throughout the survey phases of this program, general evidence has indicated that male frogs of nest species practice

reproductive territoriality and the acoustical signals are used to coordinate territorial behavior. The exact definition and biological consequences of territoriality are still somewhat controversial, but in general, reproductive territoriality involves the ability of individuals or pairs to discourage or prevent reproductive activity by rivals within a more or less definable area in space and time. In theory, such control can convey several advantages. It can help to ensure continuity of an individual's genetic line by increasing his probability of breeding. It can also allocate and secure resources necessary for survival of the brood; in addition spreading the reproductive population throughout the suitable habitat and placing the optimal resources at the disposal of the most vigorous individuals and these properly. An interesting and still controversial hypothesis is that inflexible reproductive territory size could place a fairly sharp upper limit on total population size. An additional requirement for this function would be that the amount of reproduction within each territory have an upper limit. With these ideas in mind, a series of experiments have been designed to uncover the nature, role, and extent of reproductive territoriality in Puerto Rican frogs. The coqui is a logical first species to choose for intensive study at Bio Verde Piñal Station, since it is abundant and the only species whose nocturnal activities are carried on above ground, in apparently normal fashion, within the area of artificial light provided by the station. Early efforts to study this and other species by flashlight made slow progress. Behavioral

Sequences were often interrupted by the unaccustomed light and no framework of reference was available to interpret some disconnected sequences observed. Special attention was paid to calls for several non-themes, and unusual ones were transcribed down for identification of behavioral correlates. Various methods for recognizing individuals were also developed; some had distinctive color patterns, some were toe clipped, and one small group was for a month given wristbands of tiny color-coded beads. The latter method is ideal for quick recognition at distance but requires further refinement. While behavior appeared normal and breeding occurred, lesions developed where the damage rubbed the skin. The population density of frogs within the area of the light appeared to be somewhat higher than in the forest, probably due to concentration of insect prey. The small population sample for easy identification consisted of ten adults, six males and four females, all retreating at daybreak into crevices in the separated dustmuck valley of small tool sheds adjacent to the laboratory building. No adults permanently entered or left the area during the month of intensive observation, although the population of juveniles appeared to wax and wane. Only one male, the largest, called regularly within the shed. However, one few evenings one of the two next largest males called a few times, yielding a noticeable increase of more activity by the established ones. These apparent challengers were not sustained or repeated on subsequent evenings. The largest pair of frogs bred once during the month and the second largest female presumably did; she was absent from her accustomed perch for one night and reappeared the subsequent night carrying the eggs. She must have moved into the nearby forest for eating, none of the nearby established males being monitored mated that night. When undisturbed, each adult frog moved in a fairly predictable pattern during the night. The dominant male began calling.

Minutes before Jar and called from within, or at the entrance of, his daytime shelter until about an hour after dark. The other frogs exited just before dark and often returned shortly after dusk to a nearby outdoor area, where the naturally moist bottom provided drinking water. Within an hour after dark, each frog usually appeared within a foraging (or calling) territory whose area was almost inversely proportional to the size of the frog but whose quality, in terms of insect concentration, was in direct proportion to size. The two lighted windows nearby were each occupied by one of the largest females, each female having a favorite perch in a corner from which she sprang to obtain insects alighting on the plants. The dominant male had a series of calling stations to each female

and above his shelter. An right angle corner on other shelter's edges inside the shelter led directly to the nearest 5 moves in about a route, but each was apt to be found in favored locations, often ones that seemed featureless to the human eye. The dominant male interrupted calling to take subjects on the different midnight, often moving directly into ten feet away from the shed; prey possibilities were well known. He called almost continuously, indicating that the terrain and on wet nights he could well be seen. The peculiar call shown at the top of figure 2 was heard several times. The four times it was successfully traced, the source proved to be one of the large females, those times in favored feeding areas and once in the shelter crevice, each time the female was facing a smaller frog of either sex that had entered the area. After repeating the call a few times, the larger female tilted the size of the smaller frog and called again. The intruder usually retreated a few inches after the first attack and more when it was repeated; the aggressor usually persisted until the intruder was several feet away, then resumed quickly to the favored perch. Such defense of a feeding territory was observed only in the large females; smaller females and males fed in

Apparent peace, although preferred spots seem to cover the available space fairly well. It is not yet clear whether dominance presents itself, or if feeling territories were marked, possibly with color. The call just described is termed a "warning call" from its timings, but it elicited no observable effect when played in the vicinity of frogs of either sex. Perhaps it serves merely to alert recipients. The observer has heard it in apparently complete darkness. Light revealed the usual confrontation of two frogs. The warning call, shown in Figure 2, appears to differ from the tonal call mainly in frequency and intensity, both probably due to the presence and inflation of a vocal pouch. Male warning calls exhibit a range of varying intensity and frequency, and blend at the low end of both with “warm-up” notes given in the daytime, especially near dusk and dawn, from the male shelter. Warm-up calls are repetitions of either or both of the two notes of the regular call, and have no observable behavior correlate. A slightly more intense version at night is a vocal indication that the caller will soon stop calling, but it can usually be linked in time to a regular call being given nearby, and exhibits agonistic content by analogy to the next most intense version. Take perhaps the most interesting of the territorial calls; it is given by established males from the shelter or a regular calling station when a newcomer begins to call after the established males have grown silent for the evening. When newcomers persisted in calling, the warning calls were usually followed up by attacking calls, exactly as in females, except that mates were observed to travel 10 to 15 feet to attack. Several established males coordinated strikes simultaneously and effectively silenced or drove away the newcomer. Warning calls were only given within the area of calling stations; if the newcomer was within such an area, warning calls were interspersed with attacks, while established males were fleeing or foraging away from their

stations attacked without validating relationships here were worked out by playing calls with a tape recorder after the established males stopped calling; this often stimulated the non-established males to call, setting off the chain of events described. If no male called, the established males approached the tape recorder site, attacking any other frog they encountered en route, including each other. Males with eggs in their shelters seemed to have two options in responding to newcomers; they left the shelter and began regular calling or gave the warning call, followed soon by a biting attack. Note that all of these responses served to non-established males. The response of non-calling established males to calling by other established males varied either from indifference or an occasional low-intensity warning call. Achievement of calling territory clearly involves reciprocal recognition with a series of interactions, at least at the population density of the observed group. The highest intensity (and frequency) of male warning calls is used when any other frog enters the male's shelter, particularly if large individuals are present. This is a nonsense

call, followed immediately by fierce pushing, and can sometimes be given to a lizard attempting entry. The call is most frequently heard at dawn on rainy mornings and apparently coincides with the presence of frogs that are moving into new areas and seeking shelter without knowledge of the pattern of habitation. As already mentioned, females call under this circumstance, and the calls were also given by males with shelters not lacking established territories. Intruders sometimes responded by retreating before they were attacked, although again no response was obtained to the count alone from the tape recorder. At this point, the general behavioral framework of the adult frog population appeared to be established, although case experiments can further clarify details. Three types of territorial organization are discernible: the shelter, which is

defenied by all atults; feeding territories, Unat can be base' on pact Feeding cuccecs ani cin lie at distance from the shelter, uefenie> mostly by females; and call ter- Mitories of mates, which involve Interesticne with neighbors ant have a enall perizeter of calling station but a wuch larger perimeter of area defenles. Aginiotic Lehnvicr afecting other frogs is cbeerved in the defence of eact type of territory, ani similar, probably howo- Logous, calls accompany each type of 'efense. In at lenst the dense populaticns stuliei, wales lac:iny call territories outmmbere! nales Mith thes and provide! a reprosuctive reserve, being almost surely unable to bree: before obtaining ual territenies. {vo cupporttny: experinents are relevant here; one ts a honing fexperinent ani the ther Involves restricting coveent by means of @ Sage. fo far ost hezine atailes have been performed vith established males; they hone reliably cver Ustanse up to 50 meters and seme Inalviduals returne: from 19% veters when carriel in the tame rection as a previous 5) meter Jtopiacerent, A fev fenales ani non-calling males have failei to hone vher curries 50 neters, Murther stuiles are Planned to test this type cf Fehavior, Cage stulles have provides two Important clues to the reproductive territorial behavior, "A cace male of 1/l inch mech, galvanized harivare cloth wae provided with plants, shelter, anda sisli shates 1icht bulb to attract insects throtizh the resh. The case was located about efx feet fron the shelter of an established male. One very lunge, previously established male and one non-calling young male were introtuced to the cage, Although vel. nourished, neither ale vas chie to evtablich rezwlar calling territory within the cage in six months. ack caged male has challensed repeatedly, ---Page Break--- more often than fe usa) sor noneestabl nore frequent challenges ts probably that the eaze protects then attacks ty the restient male, then either begina to call after the established sale stops, he often for the renainier of the

night, Watle the two nearest establishments males call repeatedly over the surface of the cue seating; entry routes and often butting one another, or return to their calling stations and finish out the evening in a calling trio with the caged male. There may be several reasons for the caged males' failure to establish regular calling early in the evenings: they cannot retreat far enough from the established males; they cannot attract mates through the wire and, perhaps most important, they cannot engage in physical contests with outside frogs, in which the large size of one male might confer the requisite advantage. This male has, in the past two months, attacked the smaller male in the cage when it calls, indicating that at least one attribute of call territoriality has developed. No tangible evidence of physical damage from the attacks has been found. The reason for vocal interaction between caged males and the established males outside the cage has clarified some of the acoustic mechanisms by which call territories are won and held. Observation has been supplemented with experiments where tape recordings played through a vocal outdoor speaker serve as a stimulus and the responses of a selected male are recorded in correct time relationship on the other channel of a stereo tape recorder. Three general classes of responses can be distinguished: superordinate responses, equilibrium responses and responses by newcomers. The early evening pattern of calling in E. coqui lacks the ramp pattern illustrated in figure 3, and is

strongly suspected to represent the mate attracting system. At this time little or no interaction between adjacent males can be noticed, although challenges from within the call territory apparently stimulate early development of the ramp pattern. By the time the male moves to a call station outside the shelter, a plot of call rate versus time begins to show increases and decreases in rate, with pauses beginning to appear when the rate is low. Ramping in this species is very difficult to detect with

the ear alone ~ we lack sensitivity to steep changes spread over periods of several minutes - but evidence that the fovea are very sensitive appears when we superimpose weight of interacting individuals. Rasp structure is much easier to detect in B, particularly when calls faster and whole individuals interact as large groups. Male coquettes, on the other hand, interact in pairs of trios whose pace chances and ramp durations are independent of other neighbors. The responses termed “equilibrium responses” can proceed at two levels and usually involve two neighbors, each of whose calls are louder when measured at the calling site of the other than those of any other coquette. One level is rep synchronisation, in which peaks and valleys of call rate remain in register, while calls usually shift slowly back and forth in phase, with first one animal and then the other leading. Tate sometimes gives way abruptly to note synchronisation, in which one individual drops the second (high-pitched) note and locks his first note into fixed phase with the first note of the other. Depending on temperature, the lag between leading edges of first notes ranges from about 4.08 to 0.15 seconds, which probably represents the acoustic reaction time. The pauses during low call rate periods disappear in either type of synchronization, and rate fluctuations are still further reduced during note synchronisation. Exact equilibrium during note synchronization involves a balanced exchange of the leading position; one male holds the lead for about 19 calls (20 executes a ramp, then again the other male appears and obtains the lead). The exchange point is marked by both frogs emitting the second note. Figure illustrates a pattern of exchange in which balance was not exact; this exchange was interesting because the territorial history of the males was known. The male (no. 1) which held the lead most often had been established for over a year, while the other had been calling regularly for only two or three.

veeks, Responsibility for failure to concurrently exchange the lead is difficult to assign to either frog, but the longer established male appears to interrupt often before the other relinquishes the lead by allowing some. The first two arrows mark points at which neither male produced second notes; in each case male 1 took the lead on the next note. There is other evidence of subordination in the responses of male number 2, and it is possible that the ratio of total second notes produced by each frog, 93:64 in this sequence, represents a numerical statement of relative dominance between this pair of males. Expressions of balance ranged from almost the limits of smooth exchange to situations in which note synchronization was accepted by an established male but the other male was not allowed to hold the lead for more than one or two consecutive notes. Unestablished males at times produced soft love-pitched notes in perfect synchrony with the lagging center of a pair of asynchronous, established males, but any effort to take the lead by the third frog caused the other type to immediately abandon note synchronization. Three established males were once observed in balanced note synchrony for two complete rounds of the lead. Each male produced a response while the other lagged in unison, and each altered two ranges before taking the lead; after this, one of the males could not obtain the lead again. Insight into the function of two-note calls was gained from these observations, from experiments with whistled first or second notes, and from tape recordings where frequency filters were used to remove one component. Only rapid synchronization could be obtained in response to high-pitched notes alone, or to complete calls, which is ---Page Break--- received the same response as inception of calling by non-established

males. Presentation of the high-pitched first notes alone, however, often stimulated note synchronization, particularly when played near the end of

the calling petrol, It was possible to set up equilibrium note synchronization with 4 filtered tapes when intensities, times, and temperatures were carefully matched. Evidently, an agonists message is carried by the high-pitched notes, while the low-pitched first notes provide a stimulus for synchronization, balancing responses. Several lines of evidence convince to support this view, including the high pitch of warming calls and the response to non-established males, which insulate active call responses and the withholding of note synchronization with its suppression of higher notes. The evidence came from the responses to the intensity of playback calls; when first notes alone were played, intensity was not critical over a while music, but when second notes were much lower than those of a normal call, response usually stopped altogether, sometimes for hours. These notes appear to have a cumulative effect on all males, which probably is somehow related to an integral involving intensity, repetition rate, and time. Additional subtleties were discovered in the more common type of social interaction, ramp synchronization. Besides a tendency to shift peak calling rate into register with the loudest neighbor, there seems to be an effort to increase average calling rate when interacting with an unfamiliar caller. Details of ramp synchronization interactions are still being studied, but the general pattern of this behavior can be outlined using data from 4 related species. Figure 6 shows results of an experiment that tested reactions of a single male of that species to playback of an earlier recording of his own voice. The heavy line in each pair of traces in figure 6 is the integral of call rate versus time in the tape played as a stimulus. The tape recording began at 0:00 pm, when the temperature was 21°C and the male was interacting minimally with neighbors. The dashed line in figure 6 superimposes traces recorded at the same hour the next evening, at the same temperature. This line shows the male interacting with...

established! neighbor, and the pair of tases serve as a control for competitive response when the test stimulus is not heard by the whale. Note that the call rate cycles are not repetitious enough for the minimum and made to remain in any fixed relationship. The remaining three pairs of times are responses to the stimulus tape at three different temperatures, each made at 10:00 p.m. on a different night. Temperature was 20°C in Figure 6B, 21°C in Figure 6C, and 22°C in Figure 6D. The stimulus was presented from a small speaker placed seven feet from the animal. Volume was adjusted to give the same intensity measured at the animal's call level measured at the speaker. The response was taken from a microphone placed as close to the animal as possible; this signal was filtered and resolved into pulses which were fed to a pulse height discriminating circuit, which in turn delivered a pulse to a recording ---Page Break--- ---Page Break--- device each time a present threshold was exceeded. The stimulus was represented on the chart, and playback tape recorder and chart started synchronously. Each test lasted one hour; only 36 minutes of each is shown in Figure 6, becoming 1) minutes into each test. Pair synchronization is apparent in each of the three responses; the last two also illustrate an ability to sustain or restart calls in response to stimulus variations, which of course went not in any way reciprocally responsive. One area of temperature difference either way apparently affected both call synchronization ability and absolute call rate. The figure was evaluated by measuring the area under each curve with a planimeter. Although absolute calibration of the areas was not made, the number of calls in the face of stimulus measured was about 1.74 while the greatest number of calls (response, Figure 6D) was about 3.56. Table 3 breaks down call percentages into overlapping and non-overlapping sections of the curves; it can be seen that the percentage of stimulus calls not matched by responses was very much

never effectively as response rate increases (first column) than the increase of response calls not

matched by stimulus calls (fourth column). Even the breakdown does not give the complete picture of warp synchronization, as figure 6 shows that buildup of response outside the stimulus curve is mostly synchronized with peak states in the stimulus. Although it is not apparent in the figure, there is a strong subjective impression that males of S. cogul ant, antillensie try to reach a range. Just as the interesting male is subcentine fooa che, and that this effort is thwarted in responding to tape stimuli by unpredictability of the stimulus, a tendency to overreact to small rate increase in the stimulus, and some type of limit to overall area under the curve, apparently correlated with temperature. Responses were most appropriate on the right-hand side of figure 6, where the stimulus was most regular in time. Response to a counter-responsive 2 is now being studied by level of an artificial call-pro device under control of the investigator. A theory attempting to explain the complexity of behavioral interaction in the species has been developed and is continuously being modified by additional evidence. Elements of the theory have been presented where most appropriate in the preceding descriptions. The evidence for acoustic territoriality in at least S. cog, S. aptillensi and E. hedrigki (to consider) is conclusive at this point, and other species are nearing the line of addition to the list. The nutritional requirements of the males is a year explanation for genetic maintenance of such behavior, in light of the fact that males are less territorial than females while feeding. Placement of the eggs in the center of each acoustic territory, however, does make evolutionary sense, because the eggs of other males cannot be placed within the defined perimeter and competition with the young by other young of any different genetic lineage on the same size can be minimized. Evolution appears to have

favored the development of vocalization as a weapon for territorial defense. The evolution of vulnerability to this weapon should also have been favored, since the best reproductive prognosis could be obtained by locating a new territory outside the range of existing ones. This view represents acoustic warfare as almost an extreme of the process called ritualization, or the substitution of the physically harmless exchanges for dangerous ones, as vulnerability to vocal weapons is almost completely reproductive rather than physical. The central role of daytime shelter observed in the life of E. sogui agrees with the observation that most dispersal involving a change of shelter occurs during rainy weather, while breeding occurred on dry nights as well. This, combined with the data on acoustic territoriality, provides an alternative explanation (to reproductive activity) for increased vocal activity on rainy nights. If most pale seeking new territory disperse at these times, advertisement of existing territories would serve the joint functions of defense and the filling of suitable unoccupied areas. On dry nights, the early equilibrium indicated by note synchronization of established males permits a truce which allows foraging away from the calling stations, while in this species at least, violations of the truce by resident but non-territory holding males are suppressed by physical means. To round out the theory with predictions that can be tested experimentally, female movement to males' shelters for oviposition should occur mainly in the early evening, while failures of non-established males to achieve acceptance of their calling efforts by the established males should be remembered throughout the day and inhibit early calling the next evening. Table 3. Planimeter integration of areas under call rate curves in figure 6, given as a percentage of total. nn ae pe ie Over- Tot overlapped overlapped __apoing lapping no. calls sti control 95% si wae 5th 2,000 1B tet 7 28 50 5a Pyro Lk tect 2 88

ie iy 5 3050118 test 393 7 5 at 3,660 aah ae ---Page Break--- Phase VIII - Interspecific Territoriality should briefly note the possibility that acoustic territoriality may extend across species lines, perhaps at neural intensity. An interesting possibility is that the measurement of the intensity of interspecific interaction may provide an independent quantification of the amount of overlap in ecological niche between various species, which have been difficult to study by more direct

methods. The existence of a well-developed technology for the analysis and production of acoustic phenomena makes it feasible to try to manipulate male populations with sound and analyze the results. Interesting evidence for the existence of interspecific acoustic territoriality comes from overlap or similarity between species in certain call parameters. Thus, the high-pitched second notes of E. cout, E. portoricensis, and E. axtitiensis, indicated in the section to convey arithmetical information, overlap in frequency, while the low-pitched first notes do not. Calls of the same species are still higher in pitch, and unlike the varying calls of these two species, are interspersed freely in the pattern of two-note calls. In frequency and structure they approach the calls of E. beittont, which is not too distant relative occupying the same general habitat. The two-component calls of E. enetdae and E. involve changing note duration rather than frequency and suggest that, in addition to potential exchange of territorial information with one another, communication with other species in adjacent microhabitats might be involved. In the use of arboreal shelters, E. cogui overlaps with E. hedriokt and the call of the latter bears a noticeable resemblance to the shelter-defending, warning call of the former. Direct evidence of interspecific acoustic interaction was obtained when the response of a male denning to tape stimuli was tested. This male achieved many synchronizations with taped, filtered, test notes of E. wgul, put in at least three.

experiments, responses cease! abruptly a few minutes after the start of a tape stimulus of filtered scout second notes, cavitation showed that a neighboring male coquí was robbing the responses by butting the smaller E. antiliensis male. On one occasion the invading coquí began calling from the site formerly occupied by the other male. The displaced male remained silent until the stimulus tape was finished, then began calling strongly from about a foot away on the same bush. The two males called from these positions for about an hour, and the entire exchange was recorded. The smaller male then leaped straight at the larger, which retreated the 11 feet or so into its own territory and began calling there. No further interactions were noted. ---Page Break--- Analysis of this interaction was simplified by filtering the distinctive first notes of the two species. It was apparent that nearly all calls of the first notes of the coquí, uncommonly occurred between the more widely spaced coquí notes. Figure 7 reconstructs a typical 55-second sequence of the interaction. First notes were traced from the filtered chart, so their timing is accurately shown. Line A shows the coquí calls, Line B the E. antiliensis calls, and Line C the 200-millisecond delay on phase-locked calls. Line D was first thought to represent a coquí phase-locked response, but since lag in note-synchronization of coquís has been found to also approximate 200 milliseconds, the lag in Line D appears to illustrate a property of the E. antiliensis response. This leaves no evidence that the coquí was responding at the note synchronization level, but the probability that timing in Line B was due to chance is extremely low. Note that if the lag after each call in Line B, only those calls in Line A that fell near the end of the last interval received a phase-locked response, including the actual call in Line A, which came after the speed-up of the ending ramp had inserted an extra call. This pattern of exchange was repeated with only minor variations throughout the hour of

interwetion, ‘This Interaction suggests more than one hypothesis concerning territoriality in these species. One is that the Battin; attacks are by the coqui were actually stimulated by the taped court sound that the male 2 was attacked as the only visible frog in the aves. The latter male was being tolerated at a distance at which a conspecific male would not be. ‘An alternative explanation is that the two males had reached equilibrium as if they were conspecific, and the taped sound upset the equilibrium. Although normal call structure and rates differ between the species, they were able to achieve note synchronization repeatedly by blending the most similar rates into opposition. This indicates that calling itself, allegedly suggests to be territorial in function, also serves to permit some interspecific synchronization. A small scale survey of spacing among males of these two

species indicates that some interspecific distances may be slightly shorter than intraspecific minimum distances, but in general, average distances between neighbors appear similar regardless of species. ‘The experiment is being enlarged to include all males of these and two other calling species, E. portoricensis and B. brittont in a selected area of forest reserve. These are being marked to identify the established individuals and separate them from newcomers which may or may not succeed in establishing territories. An effort is also being made to locate each male's shelter, in order to monitor reproductive success during the year. Radio tags attached to the calling males in the evenings are expected to greatly simplify location of their shelters during the day. ---Page Break--- Spucoes of sun, er a ° non ne me no PHENO OMH HOOD Pee me ‘ ts Wt HH ty ---Page Break--- When a baseline of normal spacing and activity patterns has been established in a mapped population, a number of experiments can be done. Some involve manipulation of the acoustic environment. It should be possible to “jam” the territorial communication systems in

f@ Limited area with competing sounds. Properties such as frequency and timing of effective interfering sounds can tell us much about the bandwidths and species separations in these systems. Similarly, it should be possible to create artificial territories with a loudspeaker playing either tape recorder calls, electronically synthesized artificial calls, or calls transferred from another frog elsewhere. If territorial maintenance should require appropriate responses to the real frogs, it is even possible with equipment on hand to arrange reciprocal interconnections between physically distant frogs, thereby having full control over intensities, frequencies, and other transmission properties. Sparing is also subject to experimental manipulation, as demonstrated already in the tower populations of E. coqui and E. Redrick. There, the Vasboo shelters voluntarily adopted by the frogs have been successfully moved with the residents in place. The possibilities for study of interspecific relationships in this vertical gradient are being explored. It is possible that similar techniques can be developed for holding semi-captive populations of the other species as well, and moving them about as desired. In summary, the composite populations, numbering up to nine or ten species where different habitats meet, provide one of the most challenging ecological, behavioral, and evolutionary problems in the rain forest ecosystem. The characteristics of the animals make them ideal for field study. Both in their ecosystem roles and in their potential for illustrating basic ecological principles, they appear to hold a fundamental position in Puerto Rico. References Blair, WF. 1958. Mating call in the specification of anuran amphibians, Amer. Naturalist 92: 27-51. Drewry, G.E. In Press. Factors affecting activity of rain forest frog populations as measured by electrical recording of sound pressure levels. In A Tropical Rain Forest, K. L. Auer. Aulen, B.7. 1968. Territoriality in the bullfrog, Rana catesbeiana 2968 (2): 202-213.

---Page Break--- Fella, J.B. 1963. Properties of binding gongs eliciting responses from vermitorial mules with Tat Opithel, Cone. 0:259-271. Jayela-Diaz, July 1967. Rediscovery of Buro Lemur (Cope) and additional records of reptiles from Puerto Rico. Misc. Publ. Mus. Hist. Univ. Puerto Rico, 10: 1-6. Chapman, S. 1952. A new frog from Buerets, Puerto Rico. 1é (2): 5-148, Rico. Sy Deppe. Aare Grant, Chapman, 193%. A new frog from the Virgin Islands. J. Dept. Res. Puerto Rico 26 (5): 325. Heatwole, H. 1962. Comments on the natural history of Eleutherodactylus. Heatwole, H. 1963. Revised taxonomy of the genus Eleutherodactylus. Carib. J. Gen. 3 (1) Heatwole, H., T. Merowic and 5, Oréte. 1963. Comparison of critical thermal limits of two species of Puerto Rican frogs of the genus Eleutherodactylus. Physiol. Zool. 28 (1): 1-8. Heatwole, H., P. Torres, S. to Slutite on anuran water balance: water loss by the common. Comp. Biochem. Physiol. 25 and A. Heatwole, 1969. The Dynamics of evaporative water loss in Eleutherodactylus portoricensis. Littlejohn, and A. Martin, LOE. Acoustic Interaction between five species of Leptodactylus. Proc. Anim. Behav. vt Test Ortene, GH and HF. ‘Wirts. Ecology 6th, Interspecific territories of 15. Ortans,

GH, and HS. Horn, 196), Overlap in foods and foraging of four species of Blicibivis in the potholes of central Washington, Ecology 50: T36-75. Peters, ¥. 1876. Über eine neue Froschart, Viceconsul Le Srug und Dre ‘J. Gundlach su der Insel Puerto Rico genachte Sammlung von Schmetterlingen und Amphibien, 20 wie über die Entwicklung eines Entraichiera, Hyla martinicensis Dm. Bibr, ohne Metamorphose, in natura. ‘1.k, preuss. Akad. d. Wissenschaften, Berlin, pp. T0371!) 91h. B ---Page Break--- Rivero, J.A. 1956. Two new species of Eleutherodactylus from Puerto Rico. Breviora (108): 1G. Rivero, J.A. 1963. Eleutherodactylus hedricki, a new species of frog from Fuerte Bice (Gallento, Leptodactylidae). Breviora (85): eT. Rivero, J.A. and H.L. Mayorga,

1963. Notes on the distribution of ‘some Puerto Rican frogs with a discussion on the possible origin of Eleutherodactylus locustus. Carib. J. Sci. 3 (2): 81-85. Rivero, J. A. y Maldonado, Mayorga, 1963. On the habits and food of Eleutherodactylus karlschmidti Grant. Carib. J. Sci. 3: 2-27. Sampson, L. Y. 1904. A contribution to the embryology of Hylodes bartinicense, Amer. J. Anat. 3: 475-508. Schmidt, K. P. 1927. A new tree frog from Puerto Rico. Amer. Mus. Novit. 219, pp. 1. Schmidt, K. P. 1928. Amphibians and reptiles of Puerto Rico with a list of those reported from the Virgin Islands. Sci. Surv. Porto Rico and the Virgin Islands, New York Acad. Sci. vol. 10, part 1, pp. 1-160. Stejneger, Z. 1904. The herpetology of Puerto Rico. Rept. U.S. National Mus. (1902): 549-724. Tonas, R. 1966. New species of Eleutherodactylus, Quart. Jour. Florida Acad. Sci. 28(2): 375-391. Turner, F. B., and C. S. Dist. In Press. Observations of lizards and tree frogs in an irritated Puerto Rican rain forest. In "A Tropical Rain Forest", Z. Oisun ed. Wahl, M. 1969. Untersuchungen zur Bio-Akustik des Wasserfrosches Rana esculenta (L). Oecologia (Berl.) 3: 115-155. Wiewant, Thomas A. 1969. Vocalization, aggressive behavior, and territoriality in the bullfrog, Rana catesbeiana, Copeia, 1960 (2): 276-285. 34 ---Page Break--- Appendix 1. A Key to the Calls of Common Puerto Rican Frogs 1. Regular call consisting of > notes, the second higher-pitched than the first; extra variables added near beginning and end of activity system, and two notes sometimes synchronize closely, one stating each note; all have occasional calls of 5 to 10 shorter, usually higher-pitched notes. 2. Calls seldom consist of G2 holes, in "a" they are somewhat pitched. 4. No pause between notes; noticeable constant sounds at start and end of notes ("curt"); occasional calls interspersed among regular calls; widespread habitat, weedy or shrubby areas receiving sunlight; call rate accelerating to 10 per second or higher.

seesseesseses + Hleuthenoiactylus anti lensic (Rheinhart ani leutten) 2° ‘loticable punse between notes; ne oonanrant evuni atter note: cccnstonal calls noot commun at iam ant itusit, not inter= spersed with remular calls; habitat skal in faytine ent usually on firct note; prone to repeat first note ani/er drop second; call hisher-pltched ati? ohorter than next spectec (plaintive "tiziie"); habitat restricted to nontane forest; cal! anvelerating to 2 calla per secon! iniividuele cali cynshronusly ¢> sil eflent at once sees teseeeessssees Ey Bortorloensis Sehnait 5% Ascent usualiy"dn’Jeecni 1cte; proue’te vepent both Pret notes vel: apace! ("co-gui'); widespread mut islam, cften In or ceelerating to 1 call per 4 sllences mot synchronize &. cogul, Thome oon Inman uvelLinces beeen or 4 Call introtuction sini, clear, Wieh-pitched vaintie, usually, but not always, Diloves by steep clicks of a bua. 5 W* cat not starting with an Isolwied vhictle ves. 7 > Call, unless Intermupted, a vaistie followed by nore than four clicks or 2 bis; nmentane species seseeee € 5* Call u clear whistie, eur y in the evening cfven followed ty 1 tol clicks, which wie left off Inter; chorus sounia Tike a rusty svifg; babilat lame at lov elevations 6 ehteks of cat veil separited, 5-8 per second ("pic-pie-pi: call less than 2 sec. lone: often eul1s before twilight ani after dam; habitat forest elge uni fern growth at mitaie elevations ani common everyshere at hiva elevations 7 +E, losustus Sohnsae ---Page Break--- uw qe B Clicks more rapid, approaching a buzz, 10-15 per second call lasting more than 2 sec.; moat active from 20 p. to dav; habitat forest, most common on earth banks ani nosey boulders

2. eneidae Rivero Cali composed of 3 to 10 high-pitched vhtotles; several intividuals often calt simultanecusly; 2irst 1 or 2 notes lover in pitch ani dificult to heary Lives tn forest litter layer but gometines clints to callj a snali spectes was. seseteseteees wightmanne Selmiat Notes hari to deserite as whisties and all sane frequency... 8 Sane

note repeated rapidly and monotonously for indefinite periods of time ("quick-quick-quick"); characterized by some sounding underwater; stopping abruptly or giving explosive, trilled note ("Brrr") when startled or approached by another frog; calls from concealment in muddy or nearby BEEBE Leptodactylus albilabris (Guenther) Call pattern not indefinitely regular or otherwise not as above see 9 Individual calls lasting for more than seconds; low-pitched melodious notes repeated so fast they blend into a tremolo (or trill) not easily distinguished from common call of Puerto Rican screech owl; given near edge of standing or slow-moving water + Bato marime (Inne) Call duration less than h second: 10 in cool weather calling more often and sometimes giving double or multilayered note; habitat forest floor, sometimes under stones outside forest - Be Plchnonds Ste ineger mete Call more than GneAdie tni/or expected frequently Sound of call like winding watch held against the ear or running fingernail along teeth of a stiff comb; restricted to very high elevations; calls from burrows in earth. 3, unicolor Stejneger Hot" as above! Call high-pitched chirps or squeaks with six or fewer notes per call; very small frogs Calls lower-pitched, usually six or more identical notes per call 23 Notes well spaced, very high-pitched squeaks, first call in a sequence usually one note, subsequent calls often adding notes to a maximum of 4 or 5; 2 montane, arboreal species that usually call from 6 ft. to treetop level ... Ee guyllua’Schatat 56 ---Page Break--- 13" Notes rapid in clear, trilled chirps; sequences often begin with 2 note chirps and build up to 5 or 6; widespread meadow and roadside species seldom calling more than 6 feet above the ground ittont Schmidt 2k Notes harsh and penetrating, usually given in the vicinity of fast water or waterfalls in mountain streams. E, kerlocheiati Grant Ast notes clear tones. “If call does not Zit one”

OF next two species check occasional calls in couplets 1 and 8 and suspect bind or insect sound. Bell-like "ping-ping-ping" given from tree holes in montane forest; often attributed to Mints, even heard in daytime. Hearicki Rivero, lower pitched ("ou-ou-cu") emanating from boulder pile: found in grottos in the southeastern Paniuras Mountain Range; called attributed to spirits by the local inhabitants.

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Synoptic Key to Calls: 2, two-note calls; 2 otherwise a 2 "burttick", occ. calls mixed in sunny habitat; 2 occ. call not mixed in shady habitat; 3. "Vinlte", silences synchronize, 2 calls/sec; 2, portoricensis; 3 "eo-qui", silences not synchronized, 1 call; 4 call starts associated whistle, usually followed by a click; 5 4" otherwise; 7 5, more than 6 clicks, montane; 5 4 to no clicks, lowland; 6 clicks slow, less than 1.5 sec. long, 'onepuacular'; 6" clicks fast, longer than 2 sec. graveyani shift; 7 3-20 high whistles, synchronized; otherwise low; call 8 "quick-quick-quick" = monotonic; int alarm call "bree"; 8° otherwise; 9, call longer than 4 sec., tremolo, near water; 9" shorter than sec.; 10, single "tick", long irregular interval; 10" cthervice; 11, sound like whining watch, high elevation; otherwise; 12 chirps or squeaks, tiny frogs; 12! otherwise, usually 6 or more notes/call; 13 separate squeaks, montane, arboreal; 23° trilled chirps, widespread, meadow species.

---Page Break---

We use 5 6 notes harsh, lives near mountain streams; karlachmstts notes not harsh.

"Ping-ping-ping!", tree holes, montane forest hearth. Cuscurou, boulder grottos, southeastern mountain E. cook.

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Appendix II Field Identification Guide to Puerto Rican Eleutherodactylus. Use List A as a cross-indexed key, taking characteristics in order and following instructions. Additional characteristics are presented in List B. Underlined numbers in List A refer to species in List C. List C indexes characteristics from List A and D that help confirm an.

identification, the most valuable are followed by an asterisk. Deal specimens can be identified but require more cross-checking after colors fade (skip over item 3, 5b, Se and Se). List & Yo, look at Fed Go to Cross check 1. Hind toes a. webbed b. not webbed 2. Dark luster a. from nostril to vent, a stripe upper border light, acts below b. from nostril over shoulder, well past front legs 7. The eyes absent or short 3. Tri-color, brick red, at least above tail base b. pearly white above, darker below 2. 6, ua fe. golden a) 4. yellow above, reddish below 6 aa, Ta, Bo e. gray, strongly marbled f) grey or other dark color, marbled weakly or not at all 10 4. Mostrti &, near tip of snout 5 position b. halfway from tip of snout to eye a. Underside a. as dark as back of abdomen nearly 80 5a, om b. green, or blue-green b. yellow, usually yel- lower than throat Ss be ---Page Break --- List A (cont.) he 5 6 8, Look at (cont) cantious rostralis| (one ridge from nostril to eye) top of snout (viewed from above) Dorsal coloration (heat and bask) Distance between eyes Silver spots on underside with irregular white patches Skin translucent, pair of white lines show through chin cpagie, color ivory, silver, gray or brown, fairly whitish and prominent. curving and weak Sintercesiate, hard to determine. with a thin white line. 1 euce. with a dark Tatera face. about 99 wide as jaw Truck narrower than jaw highly uniform, 13a and 16 usually true. a pattern of mottled coloration present. eso then 3/ eye-ball diameter Bell sister eye thin twice Largest toe pair width more than three largest toe pair with eye more than nostril-eye Metacarpus less than nostril-eye stance numerous, several on edge of lower lip scattered, few or none on edge of lower lip Go to Grove check be Bo, 3b, ue 3e, x oo Be, at 00 94, 10 3, by se a % 38 98, 5 List B asst ---Page Break--- ust 8 Yo. Look for If, LL. Melanophores on underside, much less dense than the underside of abdomen on throat Se, 1b (dark pigment cells, b, almost absent be,

Se use magnification 1 ¢1 present between tri-available, most use-dophorea (silver) &, 100 useful for young frogs) 4, absent between many Artiophores 3B, Se €, absent in large patches 30, 10a 12. Insite surfaces of a, dark with light spots 3a Bind less (hidden, solid red or brown 3, 8 when leg folded) 13. Width of Largest 8, more than 3/6 8a toe pads an a. bi. more than 1/2 ia, 8a, 8, 94 fraction of distance c, less than 1/2 2a, bb) Se ‘Between nostrils Lk, Light hourglass as when young. 3b, 8 pattern on back DL throughout life 5b, 94,206 15. Dark W-shaped mark a, when young. 3b, & on back of hen bl throughout life 5e; 108 16. Eyewitness jaw line in dorsal view (looking down on head) ea 17. Tedophores (silver pigment spots) absent from underside 5 Median or patzel vate lines down back and/or in legs (see list c) 29. Adults usually less than one inch long (see list ¢) 62 ---Page Break--- giiori'g "05 ssuctorttaas 6 6185 "06 M409 aT FUT st'e9 srsrtoreug “0 63646 4004ES (9 TRG Ew arie9 “2g ante sag REE 29 #96486 RETA ISIE Trrapey “E36 catag oe pe aet (36496 et oT 499¢ 9 455 TE ye 99 29056 fag 158 E45 Tes a we gT'96 ‘rg 36 W8E HOU 02g 1409 SESE Waoysa “FL 436 699 36 wet og 36 RE The G ee HOT LTS eag, TTR TT aS WEG 499 609 435 BOT prtactoy1t96 ART 29 09 Shans EE Btta6 s8aT FOTTH4EQ HBO (IS ‘TyeweTiT “FFE TT Te ‘STUIE FE “#ET 89 15S FipraseTaey EFT aaa aES Sa AT SR TARE TTS ---Page Break--- FEEDING BEHAVIOR OF THE FROGS AND LIZARDS IN THE TROPICAL WET FOREST -

PRELIMINARY REPORT Robert J. Lavigne and George Drewsy The following is the preliminary report on the analysis of the contents of the digestive systems of frogs and lizards in the tropical wet forest in the vicinity of the Fl Verte Field Station. This report covers the period October 8, 1969 to February 15, 1979 during which time 130 stomachs were dissected representing nine species of frogs and three species of lizards. Eight of the species of frogs belong to the genus Eleutherodactylus which predominates in the frog fauna of Puerto Rico. Since many of these

Species apparently compete with each other on several behavioral levels. It is of great interest to learn how they divide the available food and how their food preferences reflect their foraging behavior in the field.

Procedure: Because lizards are known to be active diurnally and frogs nocturnally, the basic assumption was made that this was the time period during which they fed and captured prey. Both frogs and lizards were identified in the field using many diagnostic color patterns that are lost when the organisms are preserved. Time of day and height of the reptile when captures were recorded were noted; in the case of frogs, it was also noted whether or not the frog was calling.

In many cases, the effect of digestive enzymes in the posterior half of the digestive tracts precluded identification of the remains of devoured organisms below the family level; the remains in the stomach were usually identifiable to species due to the method of preservation used. The procedure was to pith the frogs and lizards in the field and then immediately inject Turtox Insect Preservative into the peritoneal cavity. This caused the cessation of digestive enzyme activity, thus increasing the chances of identifying the insect remains. The animals were then transferred to the laboratory where they were tagged and immersed in a jar of Turtox Insect Preservative. Insect identifications were based on comparison with available material in collections maintained on the site.

Because of the poor state of taxonomy of some tropical insect groups, it is often easier to obtain reliable information concerning the habits of certain insects than it is to attach a scientific name to the species. Consequently, many of the species in the collection, with distinctive sets of characteristics, have been assigned letter designations until such time as scientific names become available. These letter designations, therefore, are used occasionally in tables and text.

Food Consumption Related to Taxonomic Category of Predator and Prey

Categorization of prey into taxonomic groups has been used in several recent food studies of tropical frogs (Heatwole, 1963) and of tropical and temperate lizards to provide ecological niche separation for sympatric species or to indicate resource partitioning by allopatric species (see references). Milsted (1957) suggested that it was sufficient in lizard studies to separate food items to the ordinal level and in subsequent studies insect determinations were carried to the ordinal and in some cases family level. Where this was inadequate to separate lizard species, prey volume was introduced as an additional variable. Although habitat specialization was indicated by these techniques, we believe valuable information was missed through insufficient nomenclatural separation. Additionally, this approach does not provide information on the habits of the prey species. We feel that the most effective understanding of niche specialization will come by measuring with both phenological and herpetological criteria. In order to provide comparison of our data with that obtained by various herpetologists, we have initially delineated the prey at the class or ordinal level. This information is presented in Table which is arranged according to species and

sex of adult frogs. Because present sample sizes differ according to species, the table provides the average number of each prey category per individual frog. The data indicate that, in general, the first four species contain a greater number of non-ingested contents. Interestingly, enough these four species plus E. eneludue and Leptolactylus albilabris make up the “forest complex,” whereas the rest of the species belong more properly to the open area and forest edge fauna. While this information is interesting, it cannot be used to delineate any specificity of niche feeding by predators. It does not tell us whether the insects in the order Hymenoptera were bees and wasps or ants and, if the latter, whether they were arboreal ants or those confined to the litter. Similar

Data is presented for juvenile frogs in Table 2 and for lizards in Table 3. Data are not yet sufficiently complete to allow conclusions to be drawn. Because of the way in which frogs feed, i.e., taking up a foraging site and awaiting the arrival of prey, it follows that organisms which aggregate in one spot, such as ants and termites, will be consumed in considerably larger numbers than non-aggregating insects. On this basis, we are inclined to give different weights to these two groups when interpreting our data. Lizards, while actively seeking prey, exhibit a similar pattern of behavior. A single observation...

of a fenate Anolie gtratulus closing up ante from a nest and an additional observation of selective feeding on worker termites to the exclusion of colliters by A. guuilachi suggest that these insects will have to be weighted when interpreting Lizard data as well. This is another area where nomenclatural categorization to the original level will not provide us with consistent information to make correct assumptions. Food Consumption Related to Habitat One goal of this study is to assign ecological niches to the encountered, both predator and prey, and predator provides us with a good tool, “Towan!” that enables a system of correlation that has been adopted which is a clearer but open train of associations. Initially, field observations provide us with varying amounts of evidence on habitat restriction by certain species, and such evidence continues to accumulate. Apparent absence of any species from a habitat, such as forest edge or forest, microhabitat such as the surface of leaves, trees, the litter layer, etc., of a temporal period such as day or night, when the same species is present elsewhere, is notable. The presence of an organism is also noted but is given somewhat less weight than its absence in a particular environment. For example, field observations indicate what prey species should not be available in a given niche as well as where fauna are presumably feeding. If then, as in the case of E. portoricensis which were collected on the vegetation, insects known to be confined to the litter, are found in the fenate Stomach, it indicates foraging behavior was not completely observed. Good observations receive additional testing in the field and a nucleus of species "reliable" with respect to certain ecological behavior patterns is built up. Organisms associated with "reliable" species in the stomachs of the predator with high quantitative correlation can then be assigned to the same habitats and subsequently these habitats are checked for their presence. This continues check-checking steers the investigation toward the

ven: Links in the chats Table & an Figure together illustrate a stage in the separation of arboreal and litter species both within and near the forest edge. Candidates for the List of prey indicators (Table 4), based on direct observation, were screened with respect to the feeding behavior of E. soqui, which has been observed to feed in the vegetation, and E. wightmange, which has not. Several candidates not listed were tentatively discarded. In comparing this List with that of prey items taken by E. antilensiz and E. leoustus, we discovered even shadier preferences for the same prey categories in these forest edge species. Thus, significant occurrence of a prey species in E. cogul and E. antilensig combined with relative absence in E. wightmange and E. locustus indicate

that the prey is arboreal and vice versa. The occurrence of the same prey in B. portoricensis alone would tell us little about vertical distribution of prey because feeding occurs in both niches. The List of reliable prey species suggests that L. portoricenssé females do a significant amount of feeding in the litter, even though most of the individuals collected have been taken from the vegetation. Figure 1 contains a great deal of information and requires additional explanation. The aim is to present profiles of predator feeding behavior in which times we have to uneven or still inadequate sample size are minimized. Instead of constructing conventional bar graph profiles in which the two categories of indicator species from Table 1 are presented side by side or in wedges of circles, the two profiles point towards each other. The clear attention between opposing bars indicates the proportion of prey whose vertical distribution is either unknown or complicated, by orientation alone or other gradients. Width of bars is an indicator of the prey sample size. Also, it is probable that collection toward a goal of equal prey sampled will provide more informative profiles than would the goal of equal representation by each predator species.

This technique requires, of course, that 4 different camps be constructed for each ecological setting rate, solutions of predators and prey would Table 4. Categories of prey regarded as indicators of habitat types Habitat A Litter Complex: 1) L. reot covers 2) Mollusca 8. Foreipenyte 2s 8 larvae: 3. Teopoda 9. Beolytiiae F A. Diplo 20 Strunigerye regent Chelonethie ia Etructzenys guniiachs 6. Cottenbora 1c. Festovephalus saculatus Habitat B Vegetation Complex Tipaiee Tr Ye ocotdentatse spluopteroue Larvae: Dyrtoxiphie gundTacht Lampyridae (winged) belona sp. Dolichoyo iaae Iridonyrmes nelleus iigmelachista ramon a p ‘Hvaiocorera sp, Sammamia miroyunctata Riute Pulgoriase ---Page Break--- will be consumed in considerably larger numbers than non-aggregating insects. On this basis, we are inclined to give different weights to these two groups when interpreting our data. Lizard, while actively seeking prey, exhibit a similar pattern of behavior. A single observation of a female Anolis stratulus jumping up ante from a nest and an additional observation of selective feeding on worker termites to the exclusion of soldiers suggest that these insects will have to be weighted when interpreting lizard data as well. This is another area where nomenclatural categorization to the ordinal level will not provide us with sufficient information to make correct assumptions. Food Consumption Related to Habitat One goal of this study is to assign ecological niches to the various species encountered, both predator and prey, and predator stomach analysis provides us with a good tool. To that end, a system of correlation has been adopted which works at a circular but open train of associations. Initially, field observations provided us with varying amounts of evidence on habitat restriction by certain species, and such evidence continues to accumulate. Apparent absence of any species from a habitat, such as forest edge or forest, a microhabitat such as the surface of leaves, trans, litter layer, or temporal.

Period such as day or twilight, when the same species are present elsewhere, is noted. The presence of an organism is also noted but is given somewhat less weight than its absence in a particular environment. For example, field observations indicate that prey species should not be available in a given niche as well as where frogs are presumably feeding. If then, as in the case of H. portoricensis which were collected on the vegetation, insects known to be confined to the litter, are found in the stomachs, it indicates foraging behavior has not completely ceased. Good observations receive additional testing in the field and a model of species reliable with respect to certain ecological behavior patterns is built up. Organisms associated with "reliable" species in the stomachs of the predator with high quantitative correlation can then be assigned to the same habitat and subsequently these habitats are checked for their presence. This continued cross-checking steers the investigation toward the weak links in the chain. Table 1 and Figure 1 together illustrate a stage in the separation of arboreal and litter species both within and near the

forest edge. Candidates for the list of prey indicators (Table 4), based on direct observation, were screened with respect to the feeding behavior of E. coqui, which had been observed to feed high in the vegetation, and E. wightmanii, which had not. Several candidates not listed were tentatively discarded. In comparing this list with that of prey items taken by E. antillensis and Z. locustus, we discovered even sharper preferences. The same prey categories in these forest edge species, significant occurrence of a prey species combined with relative absence in E. indicate that the prey is arboreal and occurrence of the same prey in B. portoricensis alone would tell us little about vertical distribution of prey across niches. The list of reliable prey species suggests that E. portoricensis ferales does a significant amount of feeding: Tittes, even.

thouth mest of the individuals collected have been taken Trea the vegetation. Figure 1 contains a great deal of information, and requires additional explanation. The goal is to present profiles of predator feeding behavior in which biases due to uneven, or still inadequate sample size are minimized. Instead of constructing conventional bar graph profiles in which the true categories of indicator species from ‘table 4 are presented site by site or at levels of significance, the two profiles point toward each other. The clear area between opposing bars indicates the proportion of prey whose vertical distribution is either unknown or complicated by orientation alone other gradients. Each of bare 12 = both indicators of the prey sample site. Also, it is probable that collection toward a goal of equal prey samples will provide more informative profiles than would the goal of equal representation by each particular spectrum. This technique requires, of course, that different couplings be constructed for each ecological allocation site. Reversing positions of predator and prey would provide profiles of prey behavior. Table 1, Categories of prey represented as indicators of habitat types. Habitat A is over complex A. Acarina root covers 2. Holothuria Forcipomyia larvae 3. Tephritidae Beelytine F 4. Diplopoda Strumigenys roger Jr Guetoneti is Strumigenys gundiacht { collenboits Yectocephalus maculatus. Habitat B Vegetation Complex B Battie Tr Ravens soctdentatts 2. Lepidopterus larvae 3. Gyrtexiphia quadrident 4. Lamyriaque (singe) 9. Rhabdonia sp. BY Dorotheopidae 10. Anuulocomers sp. 9. Intdorymex netleue 11. Tasmania auropunctata 6. Wrrelachists rarulonn ae, ult Rugoriaae 70 ---Page Break--- Sy ni? EXE? 38 Leptodactylus a. Boole SS SS ant, erie ¢ [ESS 0? EST OSS SJ tee? ¢ SEE 1 EXE oar & prey from sot ¢ prey from litter complex clear = unclassified vogs complex Figure 1, Profiles of predator feeding behavior 5 un ¢ eee Hse gn. 2° Eee 30 2 12 ---Page Break--- Collection Times During the early phases of this study materials were collected during

midafternoon, at which time their stomachs were full. Later collections, not as yet classified, have involved other times of day and night. “Except for those species that sleep high in the trees, the Auclig are easily collected at night. Although 2 species are often active near the station lights, all angles observed at night away from the station have been inactive. Initial frog samples were taken between the hours of 2100 and 0100. The following trends were noted: (1) Stomachs of most female frogs tended to fill earlier than those of males (2) E. wightnanae males were the only ones with full stomachs when collected while calling, the remainder of males tended to have partly empty stomachs during the period of calling, whether or not they were calling when collected (3) juveniles, which seemed to become more available for capture after 10 p.m., had full stomachs when collected, except for a single E. cogul taken with a half-empty stomach at 12 p.m. Perch Height when Collected At this time we lack sufficient data to establish whether or not male frogs forage at the same sites and times that they c Again, within range of the field station lights, E. cogui males have been observed to do so, but this may not be typical. Individuals of both sexes of E. cogui tend to establish territories within the areas of high insect density near lights, and these territories persist for long periods of time even though lights are left off. There is little reason to believe that female

frogs are not foraging at the sites where they are collected, but there is reason to believe a collection bias exists toward finding males above the ground, particularly near eye level of the collector. ---Page Break--- References Cited Hilman, Pete E. 1909. Habitat Species of native (Reptilia: icity in three sympatric Tetidae). Ecology 50: 476-481. Weatvole, #. 1963. Heologic segregation of two species of tropical frogs of the genus Eleutherodactylus. Carib. J. Sed. 31: 11-23. Medica, P.A. 1967. Food habits, habitat preference, reproduction and

Aturnal activity in two sympatric species of whiptail lizards (Ctenophorus) in south central New Mexico, Tull. 80, Calif, heals Sei. 05: 25-276. Milstead, W.W. 1957. Some aspects of competition in natural populations of whiptail lizards (genus Caenidophorus) eran J. Sei. 9: Md-hb7. Pianka, E.R. 1967. On mammalian species diversity: North American Flatland desert. Ecology AG: 353-251. Pianka, E.R. 1969. Sympatry of desert lizards (Ctenotus) in western Australia. Biology 50: 1012-1030. Rant, A.S. 1964. Zoological Distribution in Anoline Lizards in Puerto Rico. Biology 45: 745-752. Rivero, J.A., J. Naidonato and Mayorga, 1963. On the diet and food of Eleutherodactylus karlschmidti Grant, Carib. J. Sei. 30: 25-7. Schoener, Tali. 1968. Towards a theory of resource partitioning in a complex fauna, Ecology 49: 701-726. B ---Page Break--- [MH ECOLOGY OF ANTS OF GUÁNICO FOREST 11 2mm VITALITY OF HI, VEROE FIELD STATION ~ PRELIMINARY REPORT Robert J. Lavigne Much of the information gathered about the ants of Puerto Rico deals with the rove beetle species found near the coast and on coffee plantations, heeler (28) gathered some ecological data as well as describing several using his work's stay on the island. An additional species, cited by Mann (1920) and more was added to our taxonomy including by Vaceler (193!) Additional ecological information on the known species of ants was presented by Smith (1936) who spent a year in the western half of the island; he unfortunately did not have the opportunity to collect in Guánico forest. In his two-volume work on forest insects, Martorez (1954) only dealt with two species Camponotus ustus and Tymelachists razlorum. Siclsott (1946) summarized available information on the Tabin of Puerto Rican ants, emphasizing their importance in the diets of foliage lizards, Pseudothecadactylus, Eristatellus, rug! and since the complete labs show that ants may constitute more than a third of the diets of many species of frogs and lizards; at least on a North American basis, as since many ant species are

involved (Table 2), 1% Youle seen to be of interest to compile ecological information regarding certain areas that appear only in the digestive tracts of particular species of frogs and ants. Equally interesting is why many ant species appear in the stomachs of frogs which are more active at night whereas ants are generally considered to be diurnal. Prior to the present study, the list of ants collected near the El Verde field station included 22 species identified by Y. L. Brown of Cornell University (see insect checklist, Bain Forest 7). An additional species have been encountered during the last year; all have been identified to genus and most to species. A key to the species distinguished is included as Appendix 1. This key differs from Seth's (1936) key in that characters of the antennae and mandibular dentition have been emphasized in the identification of leafcutter ants usually found in the stomachs of their predators. Code names using the abbreviation "Form" for Formicidae and letters of the alphabet relate all species to previous university studies and field notes of George Drewry, resident director of the El Verde Field Station. Observations of ant activity have been made in the field whenever time permitted, noting was made as to time of day or night when ants were active as well as the type of activity in mH ---Page Break--- aust FFOIID ‘Supkeaap jo qusuoduos — G TL aes 1 enavtaw xourtuopsar Tepeoxs sopaksoee Jo 3809 poo" nOTTOL THFn ot ont : 2 prowusag poco cot = - 2 prorsed & 2 2 2 proyusos we 9 tor 2 prsTmog To @ + & - (aa) ‘as weyqporyerve os nos 1 (ae) sa wey Sg : Tyas sndosentesd, 6 on t z rae 0 iu aed _porsoop ap i Prows seca 1 Tom 8 «€ s (28) “48 syedoust0s uosous 9919 I TeRL_BS TE THE sorads uy

‘FEE AIOTOS vasss0g 2am qwotdosy aya up sopsods que upeadoo Aa poTTAAN anf puL 2zT AuoTOD “T eTaD 6 ---Page Break--- vwnich they vere engaged. Mention has been made in another report of the

attraction of cone species to fallen fruits of forest trees (table 1, p.87). These observations along with others have indicated that the following species are active diurnally: Fore Zp Fore 3 (Paratrechina sp.), Camponotus vinosus, Pheidole moerens, Formica (Rogeria sp.), Fore AY Solenopsis op., Pheidole (Solenopsis azteca pallida), Hymenachistus yaquianus and Leptogenys omithus. The workers of Iridomyrmex rufescens and Brachymyrmex heeri are active both diurnally and nocturnally, often being taken on the same tree. They have been captured foraging on the vegetation as late as 11 PM. Form CC (Paratrechina sp.) workers have only been observed to be active at night foraging on tree trunks. While workers of Odontomachus bauri can be collected singly from within the litter or under bark of trees during the day, they have only been observed on rocks after dark. The winged reproductives of these species fly at night, coming to light. Of equal interest is the knowledge as to where these ants establish their colonies. A Iridomyrmex rufescens colony was located under the bark of a living saguaro tree, Supplum laurocerasus, at a height of four feet while another was found within a dead branch of an unidentified tree. A Form CC colony was discovered living in a large hole in the trunk of a living Rhizophora mangle tree at a height of about four feet. Colonies of Pheidole moerens and Temnothorax stigma have been found under rocks in the forest trails. Apparently, the high incidence of rain in a tropical wet forest discourages some species from nesting in the soil and artifacts of the decaying forest are utilized instead by the ants. The empty seed coats of Dacryodes excelsa, Licania globosa and Sloanea berteriana serve as nest sites as well as the individual pith chambers of decayed Cecropia peltata limbs. The ant species able to use these artifacts, because of their small colony size, are Form JJ (Solenopsis azteca pallida), Fore G (Solenopsis sp.), Strumigenys rogeri, Form EE (Paratrechina sp.) and Form 2, data on colonies and colony.

site are presented in Table 1. When more information has been accumulated on the activities of forest ants, it will be possible to plug the data into the general food web and potentially answer the questions posed. ---Page Break--- References cited Mana, . 1920. Additions to the ant fauna of the West Indies and Central America, Bull. Amer. Mus. Nat. Hist. 8: hob, Martorell, Lats F. 1945. Formicidae, p. 557-60 IN A survey of the Forest insects of Puerto Rico. Univ. of Puerto Rico J. Agr. 33 (344): 692-608, Smith, MB, 1996. The ants of Puerto Rico. Univ. of Puerto Rico J. Agr. 20(4): 819-875. Wheeler, W. Morton. 1908. The ants of Porto Rico and the Virgin Islands. Bull. Amer. Mus. Nat. Hist. 26(6): 17-158. Wheeler, W. Morton. 1934. Neotropical ants collected by Dr. Elizabeth Seward and others. Bull. Mus. Comp. Zool., Harvard 77(5): ST-240, Walcott, G.N. 1948. Formicidae; ANTS, p. 810-839 IN The insects of Puerto Rico-Hymenoptera. Univ. of Puerto Rico J. Agr. 3(4): TH96975. ---Page Break--- ‘Appendix 1 Key to Formicine (workers) of the Luquillo Experimental Forest by Roberto. Laviere (Identification by Wes. From, Cornell University, Ithaca, NY; David S. Smith, Systematic Entomology Laboratory, USDA and Robert J. Lovich, Delaware Valley University of Science, Lantana, Florida). Character at page of origin 2 Kamisbles sinewe, inserted store toe borer and extending possible, well beyond border of heat 2 LI Habitably barely flattened apically, arising from corner; gut extending beyond anterior part Head ve . é 2 Abdominal yellow consisting of 4 single scales; antennae 12 segments redacted. Keel of scale concentrated into 9 single sharp points dorsally, visible with long blunt teeth apically followed by row of tiny teeth in several species; length & 2m (Form B) «+. ‘Siontomuchus haematopus’ (L.) fe; tan tibials with tiny teeth: becoming apically . ABRIGUEUS Bayh, Boery -acin: teeth other than apical parts © (Smith

ienticles; brom species; Length 1 =e (hora e} ‘Stawclvenye egpenet Moery 4 Timer border of mantt'e? Other 2 or more teeth in addition to special pair 5 teeth in a Pinn (Form FD Struntgenys roger! Reery GP Unalt teeth are brew Surunivenys gunilacht (Roger) special ptr Tenet 1 6 Frontal carinae expands intensely concealing antennal insertion; antennae ZL cemented lt nan'tblec with 5 teethy orange opectes: length 2 os, 9): a species Qyphongmmex’ rinosus’(Fpinota) ay 7 60 Frontal VAG At eral 7 Abdominal pedicel const: Le ventral or "sent 1 Redoninal piece! rons of one expanded scale or scale SES LStanSt cementie’ ---Page Break--- 10 ao! 12 we Bt uu ak Scale of pedicel vestigial or absent Scale of pedicel distinctly separated from gaster resulting in a converging to vertical scale ++ Compound eyes absent; mandibles with 6 teeth on Inner border of which mesh with the 5 teeth on the apical border of clypeus; antennae 11 segmented; orange opectes; Length 2.3 mm (Form J) sees Asblypone sp. Compound eyes present, antennae 1? segmented; mandibles with 4 teeth apically followed by row of minute teeth, 3rd tooth smaller than other three +10 Antennal scape not reaching posterior border of head; yellow species; length 2.5 mm (Form Q) Tapinona littorale Wheeler ‘Antennal scape reaching beyond posterior border of hemi; head and thorax dark brown, legs and gaster pale yellow; length 2mm (Form LL) ssesestesesеseeee Tapinona pelancephalion (Fab.) Abdominal pedicel segment, when viewed laterally, is vertically erect and as high as dorsum of prothorax; antennae 12 segmented veeeseveeee worn +12 Abtonina: pedicel segment when viewed laterally, inclined and less than height of dorsum of prothorax; antennae variable Compound eye of normal proportions, 26-30 facets; head and body bare dorsally except for scattered setae; mandibles with 6 teeth of approximate equal size; yellowish species; polymorphic: length of smallest worker, 3.3 mm, length of largest worker, 6.1 mm; (Form C) seseesesse ceseeeeee Camponotus astas Forel Compound eye

ninate, composed of 10-12 facets. B Mandibles with six large teeth of approx. equal size; each middle and hind tibiae with two spurs; dark brown species; length 2.1 to 3.5 mm (Form t) ..., Srachymesopus stigin (Pab.) Yandtbies with large teeth. All teeth much smaller than those of Trachymesopus; workers less than 3 mm in length + eyes serene. Antennal pedicel black and almost reaching posterior border of head; additional antennal segments, all tibia and tarsi dark brown. Length 2 mm. Hypoponera: trigene spactor (Forel) antennae fromish orange throughout, palpetal bases reaching posterior border of head by approximately one of its length; brownish orange species; length 5.0 mm. Hypoponera exgatanaria (Forel) axth ---Page Break--- at 6 36 wy a 18 18" 9 avr aL ar 22 eet. Antennae with 9 segments; mandibles with 5 teeth, 1, 2, 4 being larger than 3 and 5. Antennae with 12 segments; mandibles variable but not as noted. Terminal 3 antennal segments forming a club; clypeus extends posteriorly between antennal insertions; head reddish brown to black; thorax, orange, gaster black; length 2.25 mm (Form M) ....+, Wymelachicta raxutorw: Wheeler. Terminal 7 antennal segments grey, not forming a club, base segments yellow; clypeus not extending between antennal insertions; tiny yellow aspects; length 1.2 mm (Fore P). Brachyeymex heer! Forel. Mandibles with 2 apical teeth followed by 9 series of tiny teeth; head and body lacking setae; terminal 7 antennal segments grey, basal segments yellow; orange species; length 2.5 mm (Form A): Mandibles with 9 or 6 teeth. Length of antennal scape more than twice as long as distance from antennal socket to vertex. Length of antennal scape at most 1.5 times distance from antennal socket to vertex; setae of head white; black aspects; length 3 mm (reaches edge of mandibles with 5 teeth of approx. equal size. Forest not yet recorded within) (Form #4). Favatrechina

lonzicomis (latte! lie) Jianibles with'é tect, 1,2, Tana © being larger than 3 and 5; setae of hen!

Ulack; yellowien brom species; length 365 mea (FoI OC) eeveees ee + Paratreching ep. of 10710 facets; setue of with 6 teeth, 1, 2) & ant 6 being turcer than’3 and 4; yelsow species” (For’ DD) + aratrechina ntcrops (H.R, Saith) Compound eye's" normal propo-tions, 26-30 Tacete; mandibles with 6 teeth, 1,2, 4 and 6 being larger than 3 and 5 aL Head and thorax brownish orance, gaster black; Length 2 mm (Form §) . Paratrechine pose. vividula (1ylander) Head ani body une color throushout see 22 Excluding basal setae, siomsul curfuce of esotitia vith 2 sows of 5 cetues heat, toy, femur and tibia dark brows stouter species vith lieavier setae; length 2.5 mm (Form KK) : fees Paratrechina steimmetit (Forel) igeltding basal seine; steal curface of meactibia With 1 row of bor 5 setae ana one row of 3 setae; heni, boy, femur and tibia Light brom; length 2mm (Form EE)’ sess : Buratrechina op. near vividula ier) Ey ---Page Break--- 2 30 motel epines present total spines Abeent Antennae vith 11 segnent: Antennse with 12 sement, Posterior comer of hesi with cingle spines; thorex and keel of frat abieminal pelice! segment «pincee? mantities with 5 teeth; crane species: length 2.5m (Form AR)... cesses +++ Hyeocepuvus gutthi vas, boringuenste’ Vheeler Posterior comers oF heal vithout spines. 26 Epincta: spines Large ani conspicuous; frone etrlated fren nutennal foveae to posterior bonler of heal; mandibles sane coor as heal, with $ teeth; yellewish oranse species; Length 1.75 rm (Fors 2) Wanna tata (Razer) Epinotal spines barely protiulingy teens not striatedy nandibles pale yellowish with & anal brovn teeth; bead lant guster «ark brown, thorur orange, lege alnost’ trans parent; length 2 sn. oe Form FR Frontal carinse raised ani letinct reaching posterior vorier of heals heai strinte! ani veticulatess manibles with T teeth; retulsn bewn species; length 2.75 rm (Form ¥) tess Tetrmoriuy’ guineense (Fab.) Frontal curihae, if istinec,

not re: of heal, mandibles vieiables Distance vetveen epincta! svines lece than length of ones Baniibles with 5 teeth; untenme, heat, gaster and femora ‘biue black: thorax orange; tibia’ wnl tavel yellows lencth 3 mm (Fore 00) ve eevee + Hacractechia tenbellae Wheeler Distance between epinctal spines appro. 1 1/3 tines length of one; maniivie: vith = teeth apicazly fellowes by Prrower esall teeth +29 Frong not reticulate’ or atrinted; epinotal spines reiuced in size ani barely protruling: cark brow apectes Sith yellovieh brew les im (Fom 8) veeseeee . sta boringuensis’theeler rong reticulate oe 51 ‘epinota’ upines prominent; workers less than ? sm in Leth oe +30 Stristions of trons ulnoot rerehing posterior bonler of head; compound eyes normai; head and caster” iar Urewns thorax rane; iege brownish yellows length 1-6 wa (Pom). Pheltole noerens Uheeler a ---Page Break--- 30" 3 at 32 32 33 a 36" Striations oF frons not extending backwaml mich Beyond fs seticulateds sompount ‘Pheidole op. Antennae with 17 cements; manitbies vith 4 teeth, the Yast one, on ventra! amie, smell sesseesepeeeesseresereeeees 32 Antennae vith 1) cemen nes vith’ Leth, the last one, on ventral wvle, OMAlL veeseresersees 33 Firet pedicel sement evenly reuntes; heat ant gaster rettish trom, therax ani lens crange; length 1.75 wn (Form Ms) teeeteeees He iota (Jenton) Fiset pettcel sequent fiat dorsally tropphu’ of? maplaly Both front ant backs boiy blnck throughout; length 2.3 mm (has not yet been colle-tel within forest but reaches edge) (For 85) + Moncacrius carbonarium subsp. ebentmn Forel Apleal borer cf clypene with valr of distinct teeth... 3h Apical borer of elypeur larking teeth; uniform yellow 2h brow thowushowt ev-ept aplest sements of caster sorhery Levoths wees cee 8 actesa pallida tmeeler Length of smallest worker greater than 2 rm, that of Tangest worker 3. sm} peiyserphic; brown species with apteal cements or euler itcht (Fore W) spy Seigsausls'aninaia’ (hab. iS hen 6 Length’ oF conkers 1.7" Head ant guster iar* becim; thorax ani

lero orense: slightly darker than C segments basal to ity length 2.75 mm (For Wi). tevses Solenepete sp. Unters coloration tigcwthouw ov with apical segments of gaster Lighter « Dark brown species with apex 6 length of workers 1.5 1 [FOR 93) seseesese Yellow threshold or less

(For 1). faster relloss mnemonics Soienepass polynctphis length of workers T.? a Forel ---Page Break--- TP ROLR OP HOES TH TUE FOOD WER OF TROPICAL WEY TORESY - PRELIMINARY REFOR?. Robert J, Lavigne The ecological niches occupied by Insecta in the tropical wet Forest are poorly understood. In Puerto Rico the only broad study, connecting forest plants and Insects is that of Artorei! (1945) who summarized existing indices. Information has since appeared in the literature. Various trapping procedures used in the past (RIC Rain Forest Project Aun, Rep, 1967, p, 78) have indicated generalizes habitats for certain groups such as those associated with low animals. Because of the necessity to delineate the litter environment from that of the vegetation in concurrent study, a project was initiated to ascertain the ecological niches occupied by insects. The preliminary phase of this study is concerned primarily with those insects utilizing the fallen fruits of forest trees as feeding environments. The true various trees differ in the amount of flesh surrounding the seeds on the ground as well as the rate of decay of the released seed coat in those species in which this occurs. The seeds of some species such as Erysonins corlaces, Denipe axerieuna and Han Dalat are surrounded by thick fleshy pulp while these Dacryutes excelge have thin fleshy seed coats. Other species such as Inga vera and Inga agifoliy produce pods in which the seeds remain protected until the pod rots. The tough outer coats of some species, such as Sloanen tertertana, Guaren $rLehliiof plumite dehisce on the tree allowing the seeds to fall. Since the seeds are tightly compacted, thus the fruits of the

different tree: tecone available to the insect fauna in different way: As seen in Table I, a few insects have been found to be associated in some manner with fruiting bodies. Colenames using an abbreviation for the insect family in combination with a letter of the alphabet represent all species in previous diversity studies and field notes of George Drewry, resident collector of the El Verde Field Station. Interestingly, the majority of reared insects have belonged to the order Diptera and represent eleven separate families. The evidence, so far, is insufficient to ascertain whether there are restricted nest insect relationships but at least three species, Chironomid KX, Linonta willistonensis, and a species belonging to the family Drosophilidae, have been reared from two different hosts. Thus far, only these three species of ants (Formicidae), Metis goerens, Solenopsis sp. (JJ), and Pheidole sp., have been consistently associated with several fruits. Such evidence would seem to indicate that at least part of their sustenance is derived from this source. 3 ---Page Break--- ---Page Break--- Among the Coleoptera, four families (Scarabaeidae, Elateridae, Staphylinidae, and Nitidulidae) are commonly found feeding within the collected fruits. The greatest variety of species belong to the family Staphylinidae, but it is only in the dehisced and coasting of decayed achirioides that all species collected thus far have been taken. Wittia sp. A seems to have the widest host range, which is not surprising since members of its family are commonly associated with decaying fruit. Several members of the family Staphylinidae, the bark beetles, are known to occur in the forest, but little is known concerning their life histories. However, a certain predation of the fruit of the palm, Euterpe globosa, is commonly hosted by Geolytia. The pale news fare bores into by the adult vectors after the nuts have fallen into. As a result of the infestation, the entire interior of as many as 16 larvae and 12 pupae have been recovered.

lepitope terfous Jarvae (sponte: unictormined) may be coexisting in the same environment as the beetles. More should you learn about the rain forest. The He WIL will be of great importance to you. The population cycles of insects are a species of trace cone into Trait, Tuunas for the different times erroneous Cite Martorol, wate F.1. A Rite. Of the forest inaction of Puerto of Puerto Rive J. ages 39 (aa): 699608, 85 ---Page Break--- PROPERTIES OF AQUATIC COMMUNITIES IN CONTAINER HABITATS - PRELIMINARY REPORT. Joan F. Addicott? Introduction ‘The purpose of this work was to investigate some of the prominent properties of the communities in aquatic

container habitats. Some of the properties in question are as follows: Does the diversity of prey organisms vary with the density and diversity of predators in some predictable fashion? Are certain container habitats acting as near or far islands with respect to the source of colonization, and can the community structure be explained or the probability of future structure predicted? Container habitats are those in which water accumulates, usually in small amounts, in a depression formed exclusively by plant tissues, examples of these are tree-holes, bromeliads, pitcher plants, Heliconia bracts, and in general any depression formed at a leaf or plant axil. ‘In recent years these habitats have gained increasing attention from ecologists who have studied them from both a population and community viewpoint (Laessle, 1961; Maguire, 1959, 1953, 1963b; Maguire and Belk, 1957; Maguire, Belk, and Wells, 1968). ‘This interest has stemmed mainly from the realization that these habitats are very frequently small (less than 20 m^2) and abundant, and that therefore replication in the field is available, where rainfall is relatively predictable, such as in the low and middle elevations of Atlantic Costa Rica, and where it is constant, a minimal variability of the physical conditions in the habitat through time and between similar habitats in space can be expected. This lessens the probability that

Successional changes in community structure will be the result of physical changes in the habitat. This in turn makes easier the analysis of community interactions. Another advantage of this habitat for community ecology is that few kinds of organisms utilize it: osmotrophic and bacteriotrophic protozoans, rotifers, nematodes, other worms, mites, and insect larvae, particularly mosquito and syrphid larvae. The purpose of this part of the work was to evaluate and extend the ideas that Paine (1966) presented relating the diversity and density of predators to the diversity of prey. The bract contents of Heliconia bihai (1) were used for this evaluation. On the basis of the work of Maguire et al. (1966), mosquito larvae (Culex americanus) were considered as the predator and all protozoans as the prey. The Department of Zoology, University of Michigan, Ann Arbor, Michigan 86 ---Page Break--- The use of protozoans as an ecological unit is justifiable on the following basis: the mosquito larvae seem to recognize all members of the group as potential prey organisms; there are only two trophic types represented among the protozoans sampled from this habitat, osmotrophs and bacterial feeders; the protozoans are the only group found in the bracts which has a high enough population turnover rate to be able to respond quantitatively to the predation pressure. The nature of the interaction between predator and prey is hypothesized to be the following. Where mosquito larvae are absent or very rare in a bract, competition among the protozoans for the available food resources should result in a low diversity of protozoans, with the better competitors becoming very abundant, and the majority of species being rare or absent. Likewise, at very high densities of mosquito larvae, the diversity of the protozoans should be low due to the elimination of all but those species which are able to divide very quickly or are able to find some microenvironment within the bract which is relatively free from predation pressure. At intermediate densities...

of mosquito larvae it is hypothesized that the effect of predation will be to lower the competitive superiority of the better competitors, thereby allowing more species and a more even distribution of abundances among species to exist. Therefore, when some measure of the diversity of prey is plotted against some measure of predation pressure, a unimodal imbed curve should result. The hypothesis can be extended to predict the effects of added diversity among the predators and the addition of further trophic levels to the system, but since this could not be tested during this part of the work, it will not be discussed. Methods The study was carried out between June 16 and June 18, 1969 at the El Verde Research Station, in the Luquillo National Forest in Eastern Puerto Rico (the logistic support of the Puerto Rico Nuclear Center is gratefully acknowledged). The contents of

individual bracts of Heliconia vikai (2) were removed using a plastic turkey baster and rubber bulb, and placed in wide mouth jars, which had been ringed with 70% EtOH and allowed to dry. These samples were then carried immediately to the lab for analysis. The analysis consisted of taking two small subsamples, one from the top and the other from the bottom of the bottle, for censusing which protozoans were present. From the entire sample the mosquito larvae were counted and the presence of other organisms recorded. For simplicity the diversity of protozoa was calculated as the number of species present; density of mosquito larvae was calculated on the basis of the total number of larvae present, regardless of the distribution of instars among the number. er ---Page Break--- Results Figure 1 shows the results of samples taken from 35 bracts on 6 inflorescences. Use of the non-metric B and H test (Byevalling and Haniwaving test) shows that the hypothesized relationship between prey diversity and predator density was not demonstrated. Discussion A number of improvements of the methods involved in this part of the work can be made. A better measure of

Predation pressure is resirative. This could be accomplished in the following manner: in the ab, determine the relative feeding rates of each instar of the mosquito larvae (I-11); ensure that all mosquito larvae are removed from the tract during sampling (which was not the case in this study); identify each larva according to its instar. Second, with the maximum number of protozoan species found being 8, the measure of diversity of protozoans was relatively crude and insensitive. Subjective estimates of the abundance of each species (abundant, common, rare, present, absent) would enable the use of a more sensitive measure of diversity. Third, an increased sample size of bracts would include a greater range of genera of mosquito larvae, thus filling out the right-hand tail of the curve which was missing from this study. Fourth, the hypothesis as it has been presented predicts conditions in an equilibrium condition, whereas there is every reason to believe that such conditions were not always encountered. The predation pressure upon the protozoans was probably fluctuating rapidly from day to day as the distribution of individual larvae among instars changed. Some bracts may have been encountered in which colonization was not yet complete, or in which more species were present than could be supported equilibratively, and due to this, all species were still present. The effect of most of these problems probably can be analyzed during a longer-term study in which individual bracts are repeatedly sampled. Another approach would be to control the densities of mosquito larvae and allow the system to move towards an equilibrium. This latter approach will be attempted in the near future using pitcher plants instead of Heliconia bracts. 88 ---Page Break--- Buskirk, W.H. 1969. Microinvertebrate Faunas of Heliconia Flower Bracts. OPS Research Report. Unpublished. Hairston, N.G. 1958. The Species Problem in Paramecium. Evolution Kato, RJR. 1966. Protozoology. C.C. Thomas. Springfield, Illinois. 5th ed. Taessle, A.M. 1961. A Micro-Limnological

Study of Jamaican Broseliads. Ecology 42: 99-517. Maguire, B., Jr. 1959. Aquatic biotas of teasel waters. Ecology. 40: S05. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161-185. 1963. The exclusion of Colpoda (ciliata) from super favorable habitats. Tally Peraneciue transport by land. Maguire, B., Jr. and D. Belk. 196; analysis. "3, Protozool, 1: Maguire, B., Jr., D. Belk and G. Welle. 1968. Control of community structure by mosquito larvae. Ecology 49: 207-210. Paine, R.T. 1966. Food web complexity and species diversity. Amer. Nat. 100: 65-75. Shandon, 1932. Food of the protozoa. Cairo. ---Page Break--- STUDY ON THE CHEMISTRY OF THE TROPICAL MARITIME ATMOSPHERE 1. COMPOSITION OF AEROSOLS AND PRECIPITATION OVER PUERTO RICO Anders Andren and Robert C. Harris! Introduction to the tropical rainforest ecosystem chemical input through impaction of atmospheric aerosols on the forest canopy and precipitation is a major

component of the chemical mass balance. The Luquillo Experimental Forest of eastern Puerto Rico is exposed to a flow of relatively uncontaminated marine air and studies by Jordan (1969) have demonstrated that a large percentage of the sodium, magnesium, calcium, and potassium in the system is derived from atmospheric precipitation. Studies by Duce et al. (1965) have shown that the halogen composition of marine aerosols is different from the seawater from which they are derived, with many of the minor elements being highly enriched in the aerosol phase. The objectives of the present study are to determine the total atmospheric input of chloride, sodium, potassium, calcium, magnesium, strontium, fluoride, sulfate, and phosphate into the rainforest. The input mechanism will be determined by studying the relative importance of the input from aerosols on the forest canopy versus input by precipitation. Aerosol size distributions over the rainforest and variations in aerosol composition as a function of particle size.

size will be investigated, Experimental ethos Analytical procedure - The rain water samples were all concentrated under ultraviolet lamps ten to a hundred fold. Sodium, potassium, calcium, magnesium, and strontium were all determined using a Beckman atomic absorption unit. The chloride and fluoride concentrations were determined by Orion specific-ion electrodes. Sulfate was determined by a turbidimetric method. Phosphate was determined by the molybdate blue method. ‘onaruate Student and Assistant Professor, Dept. of Oceanography, Florida State University, Tallahassee, Florida, 9 ---Page Break--- Sampling Procedure ALL rain and aerosol samples were collected at the tower situated in the El Verde Experimental Forest station at an altitude of 500m. The rain was collected in 20 cm x 30 cm polyethylene containers rinsed clean with distilled water. The amount of rain was recorded for each shower as well as the duration of the rain and time of collection. The aerosol samples were collected with a six-stage Anderson cascade impactor at the same location. The water-soluble aerosols were then washed off with five to ten ml of distilled water and analyzed as described above. Results The results of the rain samples are given in Table 1. The ion ratios for these samples are presented in Table 2. The seawater ion ratios and the enrichment factor are also included for comparison. A large variation in absolute concentration is observed. This is not surprising when the many parameters which might affect the chemical composition of the rainfall are considered among which are the conditions of the sea off the coast of the island, the age of the shower when it passes over the collection site, the wind speed and direction, and the path over land that the shower has followed before reaching the sampling location. The washout effect can be seen in samples f=2 and f=2 which were from rain that occurred after several days of no rain. “The Cl/Br ratio and the Na/Cl ratio are both very close to that of seawater whereas the other ions seen

to be enriched with respect to sodium. The results for the aerosols are as follows: presented in Table 3. The 2. ALL have an initial enrichment with respect to sodium relative to seawater dating. There is a maximum enrichment in the 2 u to 6 u at Table 3. Sulfate is much more enriched in the aerosol particles than in the rainwater. 4. The total ratios of aerosol particles approximate the ratios in the rainwater except the sulfate/chloride ratio. Similar results have been found for sodium and chloride in Hawaii (Surge, 1957) but the other ions have not been investigated in the same manner and thus no comparisons can be made for other areas. 2 ---Page Break--- Sent mate Ries) le” Fates Gino chino cree ho RNCERG Crm Crna GRO epee Saw io eon 0.21" 1.65 10 oar 0.37: 0.200 0.98 0.7 wane ra sme SO EE moe ast 8 ak 20 ont oan ont 20 os Mie ope TS ES ame opt ae 058 0.08 039 000818 0008 oo TOM an teh 9h ue 00 09 20th oem 86 oe Om 1 sme S00 SOS Sm moe car sto ots ont arte o.085 vse 26 le 15 ame oe BE ame oak st 1.8 out o.ne ou oor Table 2. Ion Ratios in Rain from Puerto Rico Table No. cifta — K/Wa — Ca/fa — Me/a — F/C1_ — SO4/Cl_ — Br/Ca 18 od 0.3803 23h oie Og oe eon 9.30 be orolk 9.30 2105 oro2 0:30 188 000 0.33 ar 1.80

10-5* 0.13 0.032 2.08 0.03 0.34 0.13 92 ---Page Break--- {Whle 3, Elemental Concentration in Aerosols from Rain The same Deane mo ee = ‘ SR cat cata vale soe ‘ee wh eS wh wale? rem cole wa 0 0nT ots 8 oak Om 2505 0.50199 GOK sams Lr ay 0.050 a6 Lar otra ote Poe 06 ontee 109 235 0.8 0.55 0.260 ote Lae 90 02g 323 WS 28.55 lB O.oTh Bhs otk ons 6 aT 0.88 se O.mee oon rota, kp 252 oom nase Teo on ae Discussion The ion ratios exhibit several important features. The Cl/tia ratios show an enrichment factor of 1.12 in rainwater and 1.07 in aerosols indicating that some fractionation occurs at the sea surface. The same is true for the other elements except for Mg which shows almost the same value as that of seawater. Dry fallout could be quite an important factor for sulfate removal.

Since the S0L/Cl ratio for rain is 2.7 and that of aerosols is 13.8. Fluoride is enriched 5MO times in rain and is quite an important mechanism for input of this element into the ecosystem. Multiple samples have recently been collected and the authors hope to establish a regular sampling program in the near future. References: Duce, R.A., Winchester, J.W. and Van Nehl, T. (1965) Iodine, bromine, and chlorine in the Hawaiian marine atmosphere, J. Geophys. Res., BD: 15-1159. Jordan, C.F. (1969) Isotope cycles, in: The Rain Forest Project Annual Report, Puerto Rico Nuclear Center, Univ. of Puerto Rico, p. 26h. Junge, O.B. (1957) Chemical analyses of aerosol particles and of gas traces on the island of Hawaii, Tellus, 9: 528-537. B ---Page Break--- KARYOTYPIC STUDIES OF BATS OF THE FAMILY PHYLLOSTOMATIDAE Robert J. Boker! From 16 July to 28 July 1970, Mr. Genaro Lopez and I visited the Puerto Rico Nuclear Center's El Verde Field Station in El Yunque National Forest. Our visit was part of a National Science Foundation sponsored research project (GB-8120) entitled "Karyotypic Studies of Bats of the Family Phyllostomatidae.” Permission to use the facilities was kindly granted by PRIC and the Terrestrial Ecology Program Director. Collections were made by mist nets placed above the forest canopy and the forest floor. The karyotypic preparations were made by a modification of the in vivo bone marrow culture method. Each live animal was weighed, and then injected intraperitoneally with a 0.025% Vinblastine or Colchicine solution at a rate of 0.01 ml per gram of body weight. After two hours, the animal was sacrificed and approximately 2/3 of the humerus was removed without damaging the proximal end. The flesh and a chip of bone were removed from the proximal end of the humerus to expose the red bone marrow cavity. The shaft was flushed with 3 ml of a 1.0% sodium citrate solution, pipetting vigorously to break up any cell clumps. The resultant cell suspension was allowed to set for 10-12 minutes after which time it...

was filtered through two layers of cheesecloth and centrifuged at 500-1500 RPM for four minutes. As much of the supernatant fluid as possible was decanted, exercising caution so as not to disturb the button of cells. To the precipitate, 3 ml of freshly prepared Carnoy's fixative (3 parts Absolute methanol and 1 part glacial acetic acid) were added. Floating the materials and lipids may be removed at this stage. The cell button was gently disrupted with a pipette until a homogenous cell suspension was obtained. After allowing the cells to fix for 10-12 minutes, the suspension was centrifuged for 4 minutes and the supernatant was decanted. The cells were resuspended in 1.0 ml of fixative and centrifuged as before. This step was repeated three times. After final washing, the cells were resuspended in 1.0 ml of fixative. Three to four drops of the cell suspension were placed on a clean slide and ignited. When the fire extinguished itself, the residue was promptly cleaned from the slide. Usually, four slides from each specimen were made. The dry slides were stained with Giemsa Stain (1 part Giemsa's stock solution to 8 parts distilled water) for 15 minutes. The slides were then passed through two baths of acetone; “Department of Biology, Texas Tech, University, Lubbock, Texas gk ---Page Break--- Brief comments on the chromosomes of each species follow. Pteronotus pamellii (Gray) 2n=38, FN=60. The chromosomes of this species have

been studied from specimens from Mexico (Saker, 1967) and from specimens from Trinidad (Baker, In Press) and no geographic variation was found. The chromosomes of the Puerto Rican specimens were indistinguishable from those previously reported for species (Baker, 1967). Pteronotus fuliginosus (Gray) Figure 1a 2n=38, FN=60. This species, which is endemic to the Greater Antilles, has a karyotype identical to that reported for the other three species of Plezontus which have been studied (Baker, 1967). Monophyllus redmani Leach Figure 1 2n=32, FN=60. All autosomes are biarmed and metacentric or

submetacentric. The one of the smallest pairs has a distinct secondary constriction on the long arm. The X is a submetacentric and the Y a minute element. The closest living relative of this genus is Clossophusa, of which three species have a karyotype much like that reported for this genus (see Baker, 1967). Artibeus jansensii Leach Figure 1, 2n=30, 3100. This species has been studied from a variety of localities (see Baxter 1967, Lisle et al. 1966, and Baker, in press) and all males examined have had two Y chromosomes. This is true of the Puerto Rican specimens. There also appears to be no variation in the autosomes. Braet 2n=32 P60, all of the autosomes are biarmed and metacentric or submetacentric in nature. The X is a submetacentric and the Y is a minute element. There is a secondary constriction on one of the smallest pairs of autosomes. Sternoderms suf St.-Littatre Figure 1, 2n=30, 3100, all of the autosomes are biarmed and, except for two pairs of subtelocentrics, all are metacentric or submetacentrics. The X is a subtelocentric and the Y's are two small acrocentrics, one of which is slightly larger than the other. Broptychus bosbifrons (Miller) Figure 1, 2n=28-32, N=60. All of the chromosomes of females are biarmed elements and most are metacentric or submetacentric in nature. One of the smallest pairs has a distinct secondary constriction on the long arm. Since only females were collected, the sex chromosomes could not be determined. Eptesicus fuscus Pallool de Besuvois 2n=50, M+h8. The chromosomes of the two Puerto Rican specimens were like those described for this species from the United States and Mexico (Baker and Patton, 1967). All autosomes were acrocentric and the two X chromosomes were submetacentric. Molossus mole 2n=KNB, FN=56. The autosomes consist of a large pair of submetacentrics, three medium pairs of submetacentrics, a pair of medium-sized subtelocentrics, and a graded series of 16 pairs of acrocentrics. One of the two largest pairs of acrocentrics has a secondary constriction.

very near the centromere. The X is a submetacentric and the Y is small, but by no means minute, acrocentric. Discussion of the collections made for this study revealed some ecological aspects of the rainforest bat fauna. Tais and Yaldvieso (1970) reported several insectivorous forms for the El Verde field station. We collected 3 different genera of insectivorous bats: Peronycteris pumilio (8 specimens), Eptesicus fuscus (5 specimens), and Molossus molossus (1 specimen). Many Eptesicus were observed flying over the canopy and above the trees, and Molossus were frequently observed flying high over the forest. Fewer Peronycteris were observed, but the number collected suggests that they are uncommon in the forest. Since to our knowledge the air above the canopy had not been netted or extensively collected, about thirty feet of net was placed for one night between existing towers. The collection yielded 2 specimens of Brachyphylla cavernarum, 4 specimens of Artibeus jamaicensis, and 2 specimens of Stenoderma rufum. Of interest is the fact that Brachyphylla has not been previously reported from the Luquillo Forest, although it is known to be abundant near the numerous caves of the limestone regions of the island. On four separate nights nets were placed within the forest in situations judged to be optimal based on netting results in other tropical forests. At no time were as many as 6 specimens obtained in a 30-foot section of net. It is thus possible that a larger number of bats fly in the upper canopy than near the forest floor. 96 ---Page Break--- DPUOWOISONKYY K\)WOs a4L 40 S9dkioKs09 9Ai suorjqwog o11Aysou3 "

ar 9 ee WW WR AX RK KK RF RY RRR YE RY KRAY wnjna punepouais Aa “Yo Sarr ae OMY we ome ee XE KY WK AK We GK RK RR BY wnsouseAc2 wniykydhyso.g pt ax Roy war ” 1 ee ue MM BB ae x UR WHERE EK KK jsesdoy | o4nbiy ‘tg eww OR OR WY wor tw ax HORM RY BR BK RK Juow pas snKydouon a Ax ” eae ” vem vn ae Xe Od Xe RT KR RR smjouo seid ° € LT, vrosy we we uD neve eR ONY RY BB 227 0 WR gy 97 ---Page Break--- fone of

acetone and xylol (111) and type of xylol, and then mounted under 4 22x40 mm coverslip with Remount. A minimum of 2) specimens were counted from each specimen examined. All specimens were prepared as mise akine ap! skulls and deposited in the collection of mammals, Department of Biology, Texas Tech University. A total of 65 specimens, eight genders and three families in Table 1 were studied involving nine species. A summary of these data is shown in Table 1. Chromosomal Data for Bats From Puerto Rico @ Mw A 3 2 & sf A io & eR 5 2 56 ST AA OL é sta 7 4 Stenoderma rufa 56 Sf AA 2h Erophy tia benitrons &@ 1? 0 ou Family Yepertilontis is Eptetoue fuscus oe cs Family Molossidae Ws 6 SH A OT Even though the Puerto Rican populations are isolated, the karyotypes do not vary within species (Artibeus jamaicensis, Pteronotus parnellii and Eptesicus fuscus) which occur both on the mainland and on Puerto Rico. “Further, the karyotype of Monophyllus is much like that of its closest relative, Glossophaga (Baker, 1967) which occurs on the mainland. Pteronotus suliginosus also has a karyotype like that of other species within the same genus. These data suggest that there has been little or no karyotypic evolution within these forms since reaching this region. ---Page Break--- 4s found to have the X&/KY7¥9 sex determining ect for the number of genera to 6 (Stenoderm, Vespertilionidae, Artibeus, Choevunteus, Carollia, Euhyus) which have this type of sex determining mechanism (See Baker In Press). Baker, RJ. 1967. Karyotypes of Bats of the Family Phyllostomidae and Their Taxonomic Implications. The Southwestern Naturalist 12: hug Ht2e, Baker, RJ. In Press. Karyotypic data. William A. Kimsste, trends in bats. In: Biology of Bats. Academic Press, New York. Baker, RJ. and JL, Patton, 167. Karyotypes and Karyotypic Variation in Vespertilionid Bats, J. Mammal, 48: 270-286, Iowa, T.C., RJ. Baker, and T. vtakoJi. 1968, The Multiple Sex Chromosome System of American Leaf-nosed Bats (Chiroptera, Phyllostomidae). Cytogenetics 7: 27-38, Tonsttt, JR.

nl Dario Valdivieso. 1970, Observations on Bats and their Ectoparasites, A Tropical Rain Forest. Et, (In Press). ---Page Break--- ARRESTED SUCCESSION IN TROPICAL, TERRESTRIAL ECOSYSTEMS Jack Bvol Introduction ‘Tropical terrestrial ecosystems exposed to low temperatures or low moisture are less structurally complex than systems which are not stressed in this manner, such as the wet lowlands. Also, agricultural systems of low structural complexity (e.g. corn fields) have been notably unsuccessful in hot, wet, tropical areas, but work well in drier or colder environments. The examples of successful, permanent agricultural systems in the wet tropical lowlands are ones of relatively complex structure, such as cacao and rubber plantations, and backyard gardens in which many species of varying size are grown in a small area. Stress constitutes an energy drain on the system resulting from work done to permit survival in an adverse environment. Under stress conditions, a relatively high proportion of the energy available to a system is channeled into mechanisms which permit the system to withstand the stress, whereas systems not subjected to stress put proportionally more energy into structural complexity. In agricultural systems, an attempt to maintain limited structure is accomplished through energy inputs in the form of weeding, cultivating, and supplying herbicides and pesticides. In low-stress conditions, relatively high inputs of this form are required to avoid complexity, whereas limiting water and temperature are two natural stresses which perform the same function. What is the relative caloric cost of limiting the development of structural complexity in low-stress environments compared with areas of high natural stress? Measurements may be made to achieve the following:

1) Measurement of the rate at which systems exposed to different environmental stresses begin to return to their original levels of structural complexity after their complete destruction, 2) Measurement of the energetic cost of preventing this.

return, 43) Development of an index of structural complexity which will be applicable to a wide variety of tropical, terrestrial ecosystems: 4) Comparison of the energetic cost of limiting structure via a direct energy input vs. a specialized fossil fuel input, subbituminous coal, 00 ---Page Break--- 5) Simulation (digital or analog) of the response of various tropical ecosystems to stress and prediction of the amount necessary to prevent various ecosystems from becoming structurally complex. ‘PROCEDURES Hold study Sites - Study areas have been selected in five tropical environments: “two sites in low stress zone, two sites along a moisture gradient with mean annual temperature held approximately constant, and one site at low temperature where moisture is non-limiting. Data on location and gross climatic factors for each of the five areas are shown in Table 1. While the procedures and methods are applicable to all sites, only the Quebrada Jimenez site in eastern Puerto Rico will be described in this report. ‘The Quebrada Jimenez site is located in the Inguillo Experimental Forest and is approximately 10 km from the FRNO site at El Verde. The site has been classified as a low stress environment with respect to rainfall and temperature. The rainfall distribution in the area is relatively uniform. The vegetation at Jimenez has been sprayed with herbicides four years ago. The canopy at 19 May was open and the ground covered by a dense understory of Palicourea sp. and Psychotria sp. about 3 m tall. The soil is a moderately well-drained clay loam and the topography is somewhat irregular, with slopes averaging 20 to 30 degrees. Experimental Design - A split-plot design is being used, with four replications per treatment. Each replication consists of two main plots. “One of these was cleared, while the other was cleared and sprayed with herbicides. This initial treatment is intended to provide a measure of the role of coppicing in early recovery. Each main plot in this study consists of six subplots, two of which will be selected for measurement.

and retreatment at each of three times. One of the selected subplots will be cut and the other herbicided. Techniques - July, and September through December, 1960 were spent selecting and preparing the five sites. An area of 100 by 48 ft was surveyed at each location, with the long dimension running, insofar as possible, parallel to the contours. After the existing vegetation was felled, the five subplots, each of which is 3 by 6 m, were laid out. A 20-foot buffer zone was left around the outside border of the plots. All cut vegetation and litter was removed and discarded into the 4 m buffer zone between adjacent subplots. In the case of the Ojo de Agua plot, biomass was removed only to the surface of the deep organic layer, since this seemed to be the principal rooting medium. Due to time and labor ---Page Break--- S99 (comm x seazog 3am 300 noe oR ¥3809 TeoTdosy, 10m,8 "80 BT ap HSU Ax "320 290% fe asesoy 32% wordoasang pou0 cong onan <couguye womsaeT St tea o00E e asoiog uray ampozoduoa ony ¥3809 sew uoy reo Fdoy, row emnay 90 990 fe sam 002 9 yeatog Aa st zona ms00 woos ayuzapou .0f ot «ay soomzIMD gt 490 ook ve sero xc cruegures 09 cong o3sane moydosgans not 080 erp guawyvery (-489)(tH1) (ager seoryg —WorauAaTa Tersmr *dpooe ‘aByspteil news) 9FaBETTO 4 goaqg Tommy renny—atloz ag Seo apNaTaeL wey 8a eon ssoats UT@Is 8u3 Jo ABUTS pW WoFWVIOT “TTAB ---Page Break--- Limitations it was not possible to fell the larger overstory trees at the Quebraia Jinene, P.R. site, these were girdled and poisoned. A recent inspection indicates, however, that this treatment killed only about 20 of the trees, so an immediate retreatment is planned. Following a final reclosing of all subplots, herbicides were spray-applied to one randomly selected main plot of each replication as follows: Dow Chemical Application Trade name of Herbicide Rate (in order) i = amino - 3,5,6 = Urienloropt- covinis acts 0.067 2,4 - aichlorephenic acid 0.250 Dowpon 2,2 -

dichloropropionic acid 17kg The above doses are two to three times higher than

those usually apply in normal agricultural use. Tordon and 2,4-D are dicot killers, while Dowpon kills monocots. The date on which herbicide was applied at each site, thus the time from which all regrowth is dated, is indicated in the final column of Table 3. Preceding rotation of such subplot, the accumulated structure will be evaluated by measuring: 1) Number of stems, separated by origin (seedling or coppice) 2) Height 3) Percent cover 4) Visible light transmittance 5) Number of species 6) Leaf area index 7) Aboveground biomass. These measurements, excluding leaf area index and aboveground biomass, will also be made in nearby steady-state forests on similar sites, using Energy. A generalized energy flow diagram of the systems, using the terminology and symbols of Olum (1967), is shown in Figure 1. The drain caused by the necessity of developing and maintaining mechanisms to endure environmental stress is shown within the plant population as part of the potential generating work. This acts as feedback through a work gate on the energy flow within the plant, and its associated energy drain would increase as environmental stress increases. 103 ---Page Break--- ‘environmental survey — businesses Weicromwiom nes “Tentnieg ——vaysindeg weg e109 0m anes tse 6 $ 1 & O 13037 oindous DUBHANASOLONS-KON Nowwindos anvre ---Page Break--- S$ seq com we yeer0d 32K Teordary ato of 101.8 “D850 BT 9p ugoUT, Ir "390 coy gsorog 408 qeowdosyens —gaton ek Set THE CetQUEE epRzger st *seq ook. qeosog urmy strquoN songeroduoy eovdoxt ror 00624 sua Cony 2p ofp esa ome yeesog fea Tregures eo rdoaL, HOt Areyezopon 0g 08 ot nara foxsvouueng gt 390 ook asoroa Arq rrmguyes qwordosgang rc) 060t cone tg Sworn queuyver (+989) (60 seems (wu) opnaravt woF48901 Terry (et) (°988) “aBpTapTOH Neuse) OFWOTTD WoFIMAeTE AION 0 eyed “A¥oeid *d00907e ouoz ay aB0xD Teniy Tenuuy wes assy *S09Ts PLOTS ow Jo oaMUTTO pu WOFsMOOT “1 aTaRy, 105, ---Page Break--- ‘The cutting and herbicide treatments are shown as an outside energy source acting through a

negative multiplier (work gate) on the ‘energy flow into the plant populations. In the case of cutting, this will directly break the flow by removing the plants. The herbicide, however, acts by channeling the metabolic energy of the plant into its self-destruction; this would be represented more accurately as a source acting as a positive multiplier on the flow between the energy receptor and respiratory network of the plants. The action of hormonal herbicides apparently results from ethylene, which is produced in toxic levels (Iazlawsy and Osborne, 1969). The energy spent by a man to cut the vegetation represents the direct cost of preventing the development of structure and can be evaluated by knowing an individual's weight and the exact time spent at a given task (e.g., see Brody, 1945). The added energetic value of cutting with a machete can be determined by measuring the time required for the same individuals to clear smaller subplots of similar vegetation by hand. At least two individuals will be evaluated at each task in order to estimate the differences within workers. The application of an herbicide represents a specialized form of fossil fuel input to plant structural development. The labor used to apply it can be evaluated as above, while the energetic value of the herbicide can be measured by determining the caloric value, coupled with the dollar cost of its production. The energetic value of a dollar spent in a fossil fuel economy has been estimated by Odum (1967a). Data Processing and Simulation Some or all of the seven kinds of measurements used to evaluate structural complexity will be combined, if possible, to produce a mixed numerical index of structure. Since two of the measures are to some extent interdependent, multivariate analysis will be used to determine the contribution of each factor to plant structure. Information theory offers another possibility for combining the seven measures into a useful index, provided suitable weighting factors can be determined for each of the variables. The

Two measures of the cost of preventing structure can then be tested as responses to 1.) initial clearing by cutting vegetation, 2.) time, 3.) effect of repeated treatment, and 4.) environmental stress. It should then be possible to model the cost of maintaining a lower structure system as a function of stress, the form of energy input to control structure, and time. Further modeling may make it possible to predict structural response to stress in combinations other than those included in the field study. 106 ---Page Break--- Acknowledgement, ‘This work was jointly sponsored by grants from the Organization of Tropical Studies and an ADC Contract AT(10-1)-3656 with the University of North Carolina under the direction of Dr. Olum. The investigator wishes to acknowledge the assistance and logistical support provided by the Terrestrial Ecology Division of the Puerto Rico Nuclear Center. Literature Cited Broly, B. 1945. Bioenergetics and Growth, McGraw-Hill, NY. 1023 pp. Halloway, M. and D.J. Osborne, 1969. Ethylene: A factor in defoliation induced by auxins. Science 163: 1067-1068. A967. Safe Zone Biology. Tropical Science Center, Esta Riva, 28 Be Olum, H., 1967a. Energetics of world food production, Chap. 3 IN: The World Food Problem, Vol. III, Report of the Panel on the World Food Supply. The White House, Washington, D.C. 332 pp. Holarage, L.R. San José, Olum, HZ. 1967. Work circuits and system stress. pp. 81 - 133 IN: The Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. University of Maine Press. 305 pp. 107 ---Page Break--- PROGRESS REPORT, FIELD STUDIES ON THE PUERTO RICAN Tody, ODE vaca Kay Kepler My graduate research (Cornell University) involves the documentation of the natural history of the family Todidae, with emphasis on the Puerto Rican Tody, Todus mexicanus. This small family of birds (5 species) is one of two families unique to the Caribbean. By arrangement with Puerto Rico Nuclear Center, I have included the study area of the 51 Verde Field Station as one research site. During

the period Sept. 1968 to March 1970 I have made approximately 40 visits, studying population densities, territoriality, reproductive biology and feeding behavior. Linear densities of todies near El Verde Field Station average 12.5/ha. This area is situated in the so-called tabasco forest zone. By comparison, toady densities decrease with increasing elevation, averaging 5.6/ha in the Colorado forest zone, 2.3/ha in the terra pal forest zone and 0.05/ha in the dwarf forest zone. In lowland semi-deciduous forest densities average 20/ha and in coffee plantations 25/ha. The 160 meter fence and surveyed grid pattern of the gamma radiation study area facilitate measurements of area density and territory shape and size. Approximately 18 pairs of todies utilize the forest within the fence, giving an area density of approximately 225 pairs per km^2 (Figure 1). Comparison with Hecher's 1965 census figures for the same area indicate little change since that time. The exact territories occupied by each pair are receiving major emphasis at El Verde, allowing the area for reference. It appears that pairs remain stable throughout the year and use the same area from year to year. Territorial defense and other aggressive behavior is under study. The presence of the Black-whiskered Vireo (Vireo altiloquus) at El Verde elicits certain patterns of aggressive behavior not seen at higher elevations where this species is absent. Nests of the tody consist of burrows in vertical earth banks; a number of suitable banks occur along the El Verde trails. Much of my nesting information is being obtained here. A nesting peculiarity observed near the Tody station in 1969 consisted of 3 birds feeding young in the same burrow. It is probable that 2 of these were immature offspring from the previous year. Another facet of my study is feeding behavior. Information on foraging height, percentage of time spent feeding on insects from 198 ---Page Break--- SCALE + 1/50inc Figure! Tody +) 1988-1970 ---Page Break--- the air, from leaf surfaces and from

Other sources, and, when possible, type of food taken is compared from the 15-16 meters: Sancyy at El Verde through the range down to 1.5-meter canopies at high elevations. The study is only a

small part of the avifauna of the Luquillo Forest, and incidental to its study, information has been obtained at El Verde Station on other aspects of native birds and migrant warblers, in an attempt to understand the avian ecological relationships of the rainforest. I would like to express my gratitude to Puerto Rico Nuclear Center for permission to study in the areas.

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THE TERMITES AT EL VERDE: 1969 SURVEY

Elizabeth A. Meltahan! In July 1969, Meltahan, with the help of L.A. Burns, recensus the termite populations of the Radiation, South Control, and North Out Centers at El Verde. The work was a continuation of a study begun in the summer of 1966 and carried through the summer of 1967 and 1968. (See PRC, Rain Forest Annual Reports for 1968 and 1969. Also Olu, in press, A Tropical Rainforest). It attempted to evaluate the effects of gun variation (usage in the spring of 1968) on the termites in the Radiation Center. Two termite species of family Termitidae are prevalent in the centers: Macutitemes costulatus, which builds large carton nests on the forest floor, and Purvitemes discolor, which is not a nest builder but lives within decaying logs and stumps. Both species build carton tunnels to food sources (dead limbs, etc.). One colony of Glyptotermes pubescens of family Termitinae has been found each year in the single stump in the North Out Center. Reconnaissance surveys of nests and tunnels were made in each of the three centers. The nest survey included the area within the 80 m radius of the centers, while the tunnel survey included only the area within the 30 m radius. Few nests were sought and old nests were examined for degree of activity or abandonment. Trees and vertical stumps and trunks were examined for tunnels or tunnel remnants. Tunnels were recorded as occupied or not occupied and by which.

Termite species. The formerly active N. gostatal nests were found in July 1969, one in the Radiation Center (#12) and two in the South Control Center (#8 and #10). Nest #1 had appeared to be very feeble in 1966 (as evidenced by very low emergence of eclilere when the surface was disturbed) and it was assumed to be in the process of abandonment at that time. Another nest in the South Control Center (#9) had, on the same basis, been pronounced abandoned in 1968. In 1969 it was again noted to be active, and the tunnels leading from it were filled with termites. Nest #12 is the only nest that has "recovered" to date. *Department of Zoology, University of North Carolina. a ---Page Break--- Two new and active nests were discovered in the South Control Center (#28 and #29), plus an apparently long-abandoned one (#30) which had become exposed with the decaying away of an old stump. The two active nests were small and within a meter of each other, the first case of such proximity of nests. Figure 1 shows the sites of the nests and nest condition for the Radiation and South Control Centers in 1969. Wiegert, who had first mapped the nests of these Centers, did not similarly map the nests of the North Cut Center. In the latter, in 1965, only one long-abandoned nest was found with a 30 cm radius. After the 1967 census, a large active H. costalis nest (K) was transported to the MIE 30m radius in the North Cut Center and settled at the base of a large tree. The colony continued to be active and sent out tunnels over adjacent trees. Tunnels. Approximately 10% of the trees in each Center exhibited tunnels or remained of tunnels in 1966. This percentage has remained relatively constant, although the trees involved have changed. Tables 1 and 2 summarize the annual tunnel data since 1966 for the two major termite species at Fi Verde. The most interesting finding was the fact that in the Radiation Center, trees with occupied tunnels, which in 1966 and 1967 had constituted about 12 percent of trees bearing tunnels of any description, in...

1968 had risen to 2b and in 1969 to 55 percent. Figure 2 illustrates the rise and further shows that tunnel occupancy in the South Control and North Cut Centers did not show such precipitous rises. In 1969 all showed comparable levels of occupancy. The increase in tunnel occupancy shown by the Radiation Center was due to the presence of the new N. costalis nest that was first observed there in 1962. Table 2 shows that the percentage of Parvitemes costalis tunnel occupancy increased but little from 1966 to 1969. Another notable finding in 1969 was the large increase in N. costalis tunnel occupancy in the South Control Center and the similar decrease in P. discolor occupancy. The two new (in 1963) N. costalis nests in this Center doubtless played a part in increasing the number of occupied N. costalis tunnels. Previously both species had been well-represented in the Center. The North Cut Center has consistently had more evidence of B. discolor than of N. costalis. ---Page Break--- We are on page 58 ---Page Break--- PERCENT OF TUNNEL-BEARING TREES WITH OCCUPIED TUNNELS YEAR Fig. 2 Comparison of tunnel occupancy in the three centers at El Verde for the years 1966-1969. ---Page Break--- Table 1, Tunnel Survey Data for N. costalis in the Three Centers Trees Tunnels Trees Tunnels Trees Tunnels Year with Occupied with Occupied with Occupied Tunnels No. % Tunnels No. % Tunnels No. % 1966 90 7 22 2 2 0.0 1967 102 19 7 9.2 1968 93 3 9 10.4 4 10.3 1969 121 12 —— Survey to 20m radius only. Table 2, Tunnel Survey Data for Parvitemes costalis in the Three Centers Trees Tunnels Trees Tunnels Trees Tunnels Year with Occupied with Occupied with Occupied Tunnels No. % Tunnels No. % Tunnels No. % 1966 920 25 38.0 1967 102 8 35.0 1968 95 60 80.0 1969 80 30 37.5 "Survey to 20m radius only. ---Page Break--- Discussion In the Radiation Center only 11 original (1966) active nests were still active in 1969. In the

South Control Center 7 of the Orivinai, active nests were still active. One new nest was first observed in the South Control Center in July 1967, one in the Radintton Center in July 1965, and two (possibly representing a single colony because of their proximity) were first observed in the South Control Center in July 1969. Too little is known at present regarding the circumstances surrounding the foundation of a new colony or at least the initiation of a new nest to permit more than guesses regarding the delay in recolonization of the Radiation Center. The greater incidence of nest abandonment in the Radiation Center over that in the South Control Center has been attributed to the sterilization of the reproductives and the accompanying diminution of the population (Nethan, PRIC Fain Forest Annual Reports 1968, 1969). The evidence for this hypothesis cites the lack of nymphal forms in tunnels or participating in nest repair. Recent literature (Krishne and Weesner, 1969, Biology of Termites, Academic Press) has caused a re-evaluation of this interpretation. The termite genus Nagutitemws is reported to have two lines of definitive workers, large and small, neither of which gives rise to the other. Nymphs, which are immature individuals with wing pads in the alate (reproductive) line, do not normally participate in foraging, nest construction, etc., and should not be expected to be encountered at these tasks. The group that appeared to be lacking in the irradiated nests, then, was not necessarily the nymphs, but the small worker group, previously mistakenly called "nymphs." The basis for their apparent absence is not understood. Since all workers often give rise to the soldier caste, I.A. Durns has suggested (personal communication) that perhaps a stress such as radiation (resulting, perhaps, in loss of reproductives) triggers the excessive development of soldiers from small workers, thus using up the latter. Perhaps this comes about through lack of a phenotypic interaction with reproductives which permits.

this excess of soldier formation beyond the ratio limits usually characteristic of the species. In possible support of this view is a termite colony from outside the experimental areas, studied in July 196x. It was a nest in relatively poor repair and only moderately active, and it was chosen as one

possibly in the early stages of abandonment. When it was found to contain two empty royal chambers, one in an older nest section and encrusted with fungal growth, and the other in the more recent and active part of the nest, no royal partners, no brood, were detected in any part of the nest. A large number of white soldiers were observed in the stage just preceding the adult soldier stage, indicating possible soldier flare. Samples of the inhabitants of this nest were taken in order to compare the ratios of all types of individuals with those for a normal nest containing a king and queen. If it shows a deficiency of small workers but an excess of soldiers and white soldiers, it may support the hypothesis that small workers may tend to decline in favor of soldier increase in stressed nests on their way, perhaps, to abandonment. This comparison has not yet been made. If any case, the Radiation Center is now comparable in termite tunnel occupancy to that of the other two Centers. Careful searches of the Centers out to 80 m should be conducted to document the probable re-invasion of colonies into the areas where nests have been abandoned.

POLYETHISM IN WORKERS OF NASUTITERMES COLOLANUS (HOLM) Elizabeth A. Metcalf. Polyethism within the termite worker caste, similar to that reported for honey bees (Thompson 1952, Ribbands 1952), bumble bees (Free 1995), Halictid bees (Batra 1964) and ants (Weir 1958a,b) has been suspected for years (High 1922, Grasse and Yolrot 1950, Kashoven 1958). The experimental investigation, however, has been recent (Castes 196x, Horse 1368). In the tymenoptera, worker job preferences have typically been associated with worker age as well as with solitary need. This

association has also been initiated for termites. Pasteets observe that in Nacutivermeg Iijee (family Termitidae) (family Ternitiéae) older Feage Tniividuats of both the small and the large worker Lines have really ventured outside the nest and hence tended to be foragers. However, working with species without a definitive caste, Zooteraopels nevatensis (family Hotctermitidae), reported that as the initial variety progressed from young larva to nymph it tended to spend more time at colony maintenance and less in trophallaxis. The present paper reports a behavioral difference within the worker caste of Nasutiternes costalis (Holmgren) similar to that reported by Pasteets. Also a member of family Ternitides, this species has both large and small definitive workers which presumably represent separate lines, neither giving rise to the other. In caste makeup and development, N. costalis is assumed to be similar to N. arborum described by Noirot (TIS), to N. lujae described by Pasteets (1905), and other masters of the genus. Workers in both the large and the small lines are presumed to continue to molt and thereby to represent at least three different age stages of large workers and at least two age stages of small workers. In other species, these stages have been differentiated on the basis of pigmentation, certain morphological characteristics, and sex (Noirot 1995, Weester 1969, Pasteets 1965). Although no biometric studies were carried out with N. costalis, the workers could be readily separated into the stages indicated, chiefly on the basis of size and head pigmentation. The study was carried out in August 1967 in a montane rain forest in northeastern Puerto Rico at an altitude of about 450 m. It grew out of an investigation of the effects on natural populations of termites of gamma radiation from a 10,000-curie Cs-137 source exposed in the rain forest for 93 days in the spring of 1965. It was part of a large study sponsored by the United States Atomic Energy Commission through the Puerto Rico Nuclear

Center (Otun, 1970 In press). 1. Carton nests were abundant in the area and were almost invariably on the ground. Local nests, except when in the process of expansion, had intact surfaces, at least over occupied portions. University of North Carolina, Chapel Hill, North Carolina ---Page Break--- Part of the radiation study involved comparison of speed of pest repair in irradiated and non-irradiated colonies. When a coal hole was punctured in a nest, the immediate reaction of

the termites in the vicinity of the breach was a precipitous flight, domeward into the interior of the nest, except the soldiers (headworkers), which, in contrast, rushed to the opening. Some of the soldiers flew out over the exposed surface, running erratically about with route letters. Gradually their activity subsided, and after a lapse of four minutes, if no further disturbance was forthcoming, they retreated into the opening but continued to keep their heads pointed outward. No workers of any type were seen near the hole for about five minutes from the time the breach was first made. Then one by one, workers would appear and begin to repair the hole by daubing fecal material (carton) on the broken materials. It was soon noted that the termites which returned to begin the task of closing the hole appeared almost always to be large workers. This observation led to an attempt to obtain quantitative evidence for this apparent behavioral difference between the members of the two worker lines. Series 1: Preliminary tests of nest repair were carried out on 9 different nests between August 19 and August 23, 1967. Five had been within a few meters of the radiation source and four had been at distances greater than 80 m. Nests closer than 40 m had all been abandoned by August 1967. None were in the process of expansion when sampled. Sampling from an opening (1 cm in diameter) punched in the nest surface was made with an aspirator having an intake tube 5 mm in diameter and occurred within 10 minutes of the breaching disturbance. After

a number of respiring workers pad congregate! All the whole a sample was taken by placing the separator intake tube at the opening and aspirating quickly all termites possible. Average aspiration time for a single sample was two seconds; after this time only soldiers were available, all workers having fled inward. Usually from 5 to 15 workers, plus a greater number of soldiers, were captured in each sample. About 10 separate samples, with intervals of about 10 minutes between, were taken at each nest. Each sampling disturbance set up the sequence of soldier-out-pouring, gradual subsidence of soldier activity, and eventual emergence of workers to begin repairing. ---Page Break--- ALL termites aspirated from a single nest were preserved in a separate vial of 70% alcohol and were later identified to type. Results Table 1 gives the sample composition by nest. The nests are separated according to their distance from the radiation source. The data indicate that although average numbers of all types of termites captured at disturbed surfaces were slightly less for hosts in the irradiated than for those in the non-irradiated area, percentages of soldiers, large workers, and small workers captured were similar for the two. In both cases large workers (mostly third stage) constituted about 90% of the workers captured. The low percentage of small workers (and of first and second stage large workers) at the breach implied a possible tendency for them not to take a prominent part in nest repair. Observations of spontaneous expansion of nests, however, showed that small workers appeared to be as much involved in the construction work as large workers. Therefore the hypothesis was considered that large workers (mostly third stage) do not do the surface repair work following disturbances, while both large and small workers expanded the nest. Test series 2 tested this hypothesis. Series 2: Expansion versus Repair Procedure These tests were conducted on August 26 and 27, 1967. They involved 3 of the previous nests plus

additional nests. Two were sampled twice (on different days). All nests sampled were selected because they were in the process of spontaneous expansion, with workers working busily at openings they themselves had made in the nest surface. Expansion holes, like the punched holes, averaged about 1 cm in diameter. Without prior disturbance, one quick (2 second) aspiration was made at an expansion hole at a given nest. The workers were counted immediately and preserved in labelled vials, along with the simultaneously aspirated soldiers. An artificial hole was then punched on the same nest, at least 6 inches from the expansion site. As fast as workers appeared at this punched opening, they were captured and preserved, one by one, until a total had been reached approximately equal to the number aspirated at the expansion hole. The aim was to

compare worker composition under the two sampling conditions. 120 ---Page Break--- TRL nets' Ma Steet ef * hom oe e @ 1m + & 6 1 9 3 wp w @ wrt bm wo mw 8 0 tm a wom 8 0 eo me me a a mee Oe 6 La mete es Ls 88 mes Sig tin nae re ner Tee on a er Wid Seo wt tae meer fe Rive sage soit war Sih Pew eager er etter a 'StS NESE os kr em wey oe to pen aS Bn or ee me me Strate types a se abe ---Page Break--- Results Table 2 presents the data. Four sets of collecting vials were used in the study and their data are given separately to show consistency of results. Vials IF and 18 represent, of course, one group of 9 nests; vials 26 and 28 represent another group of 10 nests, etc. While nearly half the "expander" workers were of the small type, only about 17% were of this type among the "repairers". There were, in fact, smaller percentages of all types of workers at the repair holes except for third stage large workers, which increased from 0% to 89%. Soldier capture was also greater at repair holes, a predictable result, because of the continued disturbance there. At expansion sites, first stage small workers exceeded in numbers even third stage large workers. The expansion site data and the

Similarity of worker composition of the repair hole samples to that of the samples of Series 1 appeared to support the hypothesis that small workers tended to expand nests much more readily than to repair them. A more likely hypothesis, however, concerned the alacrity with which they emerged to commence nest repair following a surface disturbance. After one of the nests in Series 2 had been sampled, it was examined again more than an hour later. The artificial hole was still being repaired, and now small workers were seen to be much in evidence. It appeared that they repaired nests as diligently as they expanded them but were merely shyer than large workers about returning to a disturbed area. A third test series explored this hypothesis, Series 3: Delayed Repair Procedure. This series (August 27 and 28, 1967) studied the effect of waiting for 50 minutes or more after a perceiving disturbance before making one quick (2 second) aspiration of the termites that had come to make repairs. Ten nests were sampled. Results: The total sample composition (Table 3) was similar to that of the nest expansion sample (Table 2). The data show that large and small workers participated in repair to a comparable degree when there had been no surface disturbance for 50 minutes or more. Like the expansion data, they show that first stage small workers (WSL) were as prominent as third stage large workers (L3) in nest construction. ---Page Break--- Table 3. Sample Composition of Termites Taken from Repair Holes 50 Minutes or More after a Disturbance, No. of Termite Types Tests 7 3 Me Hse Wg, 0 6 np ww 7 Ble ut 3 Table 4. Comparison of Proportion of Worker Types in a Natural Colony with that of Workers Participating in Disturbed and in Undisturbed Nest Construction. Worker Types re Mase Wt Total Nest population 719.575 535137 aaa. 0. Dhak 22.5% 8% U7. Recently disturbed construction 87.56 2.9% 0.8 5.58 3.38 Non-disturbed construction 29.26 13.9% 10.56 15.6% 30.9% Termite types are in Table 1. 123 ---Page

Break--- Comparisons of Worker Types Engaged in Construction with those in a Mature ¥. costalis Colony Differences in proportions of worker types captured at both disturbed and undisturbed construction sites indicated that behavioral differences existed. In order to evaluate properly the relative participation of each type, however, knowledge of its respective number in each of the colonies sampled would be desirable. These numbers are not known. However, the entire population of another i. costalis nest from the same general area was analyzed for colony composition. All the termites from the nest were pooled in a large container of 70% alcohol. Five independent samples, totaling 2361 workers (plus soldiers, alates, and immature stages) were analyzed. The table shows the average percentage of each type of worker present in the nest. Standard deviations for these data (using the arcsine method for transformation of the percentage figures) did not exceed 0.2 percent in any case. The colony had been large and active, with a royal

pair and brood, so its population was assumed to be typically constituted. Table 4 compares the percentages of each of the worker types found under the following three conditions: a) in the nest population as a whole, b) participating in nest construction (repair) under conditions of recent disturbance, and c) participating in nest construction (expansion and delayed repair) under conditions of non-disturbance. Chi-square evaluations of the data, taking the frequency distributions of two of the conditions at a time, gave highly significant probabilities (0.0001) that the three sets of data were not homogeneous. In other words, the data indicate that significant differences in behavior relating to nest repair were elicited from different termite types under the conditions of the tests. Discussion The data support those of Pasteels (1965) who studied trail laying in W. lajae. He found that older stages in both the large and small worker castes were more venturesome than younger stages.

The heat construction data for K. costalis similarly showed that third stage large workers (*L3) far exceeded all other workers in the alacrity with which they arrived at a surface breach to begin repairs. Although much fewer in number, second stage small workers (#52) were ext most venturesome. First stage large workers (Wit) were especially reluctant to carry out repairs. The data also indicated a possible tendency toward "Job preference" that may be distinct from differences in readiness to confront alarming situations. While W3 workers at undisturbed construction sites were present in about the same percentage as their assumed number in the colony (30%), the other large worker stages (Wg and Wr) were present at only about half their "expected" percentage. Both small worker stages (Wisp and Wis1), on the other hand, nearly doubled their "expected" participation. This greater tendency of small workers, in the absence of disturbing conditions, to participate in nest construction may be an example of a true division of labor among termite workers. Summary: A field study of colonies of Nasutitermes costalis in a montane rain forest in Puerto Rico indicated that third stage large workers returned much more readily to nest surfaces to make repairs following a breaching disturbance than other worker types. Where no recent disturbance had been (or was an hour past), small workers, constituting (presumably) only about 2% of all workers in a nest, composed over 80% of the workers collected at the construction site. These findings are evidence of polyethism within the N. costalis worker caste. Acknowledgments: This study was supported by the United States Atomic Energy Commission, through the Puerto Rico Nuclear Center. L.A. Burns aided in sampling the N. costalis nest for colony composition. Bibliography: Batra (W.W.), 1964, Behavior of the social bee, Lasioglossum zephyrum, within the nest (Hymenoptera: Halictidae). In Sociobiology, p. 159-186. Free (J.B.), 1955. The division of

Labour within bumblebee colonies. Indectes Sociaux 2, p. 195-211. Crasée (P.-P.), and Notrot (ch.) 1950. Documents sur la Biologie des Guentoterses magéuienge n. ep. Ann. Se. Hat. Zool., Parke 1° SS Hogh (E.), 1922, Les Termites. Imprimerie Industrielle et Financière. Bruxelles. Howse (P.B.), -On the division of labour in the primitive termite Zootermopsis nevadensis (Hagen). Ins. Soc, 155 p. 45-50. Kalshoven (I.G.), 1958. -Observations on the black termites, Tospilalitelmes app. of Java and Sumatra, Insectes Sociaux 5, p. Lindauer (M.), 1952. Ein Beitrag zur Frage der Arbeitsteilung im Bienenstaat. 2. vorgl. Physiol. 3h, p. 299-246. Foirot (C.), 1955. Recherches sur le polymorphisme des Termites supérieurs (Termitiinae), Anz. Sei. Mat. Zool. Biol. Animale TL 27, 399-595. Dum. (H.), ed Comm esi 2970. A Tropical Rain Forest. U.S. Atomic Energy 1p press. Pastels (J.), 1965. -Polyéthisme chez les ouvriers de Nasutitermes Yujae (Termitidae Isopteres). Biol. Gabonica 1, p. 101-205. Ribbands (C.R.), 1952. Division of labour in the honeybee community, Proc. roy, Soc. B. 140: 32-43. Wessner (F.N.), 1965. -The Termites of the United States, A Handbook. at, Pest Control Assoc. Elizabeth, N.J. Weir (J.B.), 1958a. -Polyéthisme in workers of the ant Myrmica. Part II. Ins. Soc. 5, p. 315-339. 126 ---Page Break--- OCCURRENCE

AND DISTRIBUTION OF AQUATIC FUNGI, IN THE EL VERDE FOREST: A PRELIMINARY REPORT. By Alan Seymour. Except for a report by Rocsy-Vallerrana (1956), the aquatic fungal flora (Phycomycetes) of Puerto Rico is unknown. This report, while describing three new taxa and extending the distribution records of fifteen existing species, is at least exclusively with terricolous forms. Opportunity was afforded between November 10 and November 16, 1969, of obtaining from the El Verde forest, collections of soil and water which might yield aquatic fungi. The results of this preliminary survey were quite promising since out of a total of 265 collections, 226 isolates.

were obtained, representing thus far 8 genera and 2 species. Since specific determinations have not yet been possible in all the resulting collections, a complete taxonomic account will appear in a later report. Materials and Methods Techniques for collecting and isolating Phycomycetes fungi are well established (Johnson, 1956; Sparrow, 1960; Scott, 1961; Seymour, 1970). Samples of wet and dry soil were collected in 35 ml. polypropylene bottles and returned to the laboratory within three hours of collection. Approximately 10 g. wet weight of soil was placed in a sterile Petri plate and covered with distilled water to a depth of about ten. After the particulate matter had settled, various baits (boiled halves of hemp seed, pieces of snake skin, shrimp skin, cockroach wing, and pine pollen) were added to each culture. The gross cultures were incubated at 25-28°C. Each piece of bait was examined periodically with the aid of a compound microscope after the third day of incubation. Water samples were taken in the same manner, except that each 35 ml. sample was diluted with 10-15 ml. of distilled water before baiting. Continuing studies; financial support from the National Science Foundation (Grant GE-1310h) is acknowledged with gratitude. *Department of Biology, University of Pittsburgh, Pittsburgh, Pennsylvania, ---Page Break--- Collections of algae, insect exuviae and submerged plant debris (leaves, stems, fruits, seeds) were returned to the laboratory in sterile plastic bags and examined microscopically. After examination the material was placed in individual Petri plates, covered with distilled water, and allowed to incubate for 3-5 days. The material was periodically examined after the incubation period. Since the primary objective of the survey was to obtain living isolates of the Saprolegniaceae, no attempt was made to isolate or culture other forms encountered. The Saprolegniaceae species were isolated and propagated in unifungal culture on hemp seed and returned to the investigator's laboratory for

Future work. Beoults and Di Wseson Collections were made of wet soil from the edge of the Rio Sonadora and from various streams and temporary pools throughout the forest. Soil samples were also taken from diverse ecological habitats along paths, open areas, around roots of vegetation, under rocks and vegetation, and under forest litter. Fungi were found in 57 of the 110 collections made. In addition, 35 soil samples were collected, air-dried, packaged, and returned to the investigator's laboratory for subsequent examination. All samples have yielded species of aquatic fungi. Water samples containing sediments and debris were taken from the Rio Sonadora and from various streams and pools. A survey for fungal substrates was also made at these locations. A few bits of driftwood and submerged leaves were found, examined directly for typhomycetous fungi, then incubated as previously described. This material yielded no species of aquatic Hyphonycetes. The river, streams, and pools were also carefully searched for algae and insect exuviae. Several species were detected following incubation of this material. Inasmuch as no studies of aquatic fungi of the #1 Verde forest have been made prior to the present one, no general conclusion may yet be formed. There are, however, a few points of interest in connection with this relatively small number of collections, although the latter cannot be considered to offer more than a fragmentary picture of the regional flora. Little evidence has been found of a large or unknown tropical flora. On the other hand, a number of genera are particularly well represented and call for intensive investigation in tropical laboratories. The lack of certain genera (Alaonyces, for example) common to tropical

regions may perhaps be attributed to the wetness of the soil. Future collections will undoubtedly yield many species suspected to occur in this region, but which are as yet uncovered. 18 ---Page Break--- Sum of the 265 collections of soil, water, and organic debris made in the El Verde.

forest, 206 isolates of aquatic tunnel representing, thus far, 8 genera and 22 species were obtained.

Literature Cited

Johnson, T.W., Jr. 1956, the genus Achlya: morphology and taxonomy. ado pp. 22 pls, Univ. Mich, Press! Ann Arbor.

Rosay-Valderrama, C.R. 1956, Some water molds from Puerto Rico. 3. Elisha Mitchell Sci. Soc., 72: 129-137, figs. 1-29.

Scott, W.W. 1961. A monograph of the genus Aphanomyces. Tech. Bull. ASL, Va. Agr. Exp. Sta., 95 pp. 9 pls. Virginia Polytech. Inst. Blacksburg.

Seymour, R.L. 1970. The genus Eaprolenta, 123 pp., 18 pls. Chaner, Jere, Germany.

Sparrow, F.K., Jr. 1960, Aquatic Phycomycetes. 2nd Ed., 1187 pp., 1 pl, 51 figs. Univ. Mich. Press: Ann Arbor.

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RADIOTRACER STUDIES OF NUTRIENT CYCLING

Nellie Stark#

Abstract

Studies on the depth of efficient nutrient uptake by second growth and climax vegetation show that Cecropia peltata, the second growth dominant tree species, is deep rooted and able to take up nutrients from 1.0 m depth. Guarea trichilobata, Dacryodes excelsa, Heliconia spp. and Piper latifolius are shallow rooted with limited capacity for taking up nutrients from shallow depths. Young Sloanea berteriana and Mant. nitida are deep rooted, absorbing nutrients from 0.5 and 1.0 m depth. While near-mature specimens develop a surface feeder root system capable of taking up nutrients from 0-6 cm depth. In studies of the pathway of nutrient cycling using young saplings with mycorrhizae, it was found that all tests with ^29P, ^65Zn, and ^69Zn showed an initial increase in the radiation level in leaves and roots during the first month. Since rhizomorph was scarce during this rainy season, it is possible that heavy rains leached the isotope from the litter or humus. Collection of soil animals and fungi showed that these agents are important in nutrient cycling on Puerto Rican Latosols. Increases in the radiation level of the humus were usually coincident with increases in radiation level in the roots, suggesting that the humus is the main source of nutrients for surface roots. No positive

Evidence for direct nutrient cycling on Puerto Rican latosols was found. Introduction Studies by Went and Stark (1968a, b) described the direct nutrient cycling hypothesis which states that on the

poorest soils in the tropics, nutrients are removed from dead organic matter by mycorrhizal fungi and are transported through rhizomorphic tissue to living roots, thus by-passing the soluble phase of nutrients in the soil. Direct nutrient cycling is recognized as only one of several possible nutrient cycling pathways. It is thought to operate most efficiently on white sand areas where the mineral soils are too poor in most biologically important elements to support the lush rainforest which grows there. In this type of rainforest, the bulk of biologically important elements is held in the organic phase of the ecosystem, and nutrient transfer appears to be from dead organic litter to living roots (direct), rather than from the soil solution to roots (indirect). ‘Desert Research Institute, Univ. of Nevada, Reno, Nevada ---Page Break--- If direct nutrient cycling is functioning, then much of the uptake of elements must be from the litter or upper 1-3 cm of soil. Observations suggest that direct nutrient cycling may occur in many other ecosystems in a modified form. Other pathways of nutrient cycling include breakdown by soil animals, bacteria, and free-living soil fungi, with uptake from the humus or soil solution. To test the hypothesis, radioactive tracers have been used in greenhouse studies of potted plants at the Desert Research Institute in Reno, Nevada, with field extensions of this work at the Puerto Rico Nuclear Center. The Puerto Rico studies were primarily field tests of the greenhouse methods, with modifications designed for the specific field problems. One test determined the depth from which nutrients are taken up from the soil by the roots of second growth and climax vegetation at El Verde. The other tests methods to describe the pathways of nutrient cycling which predominate on the latosols at Pi

Verte. ‘The objectives of this work were to test the use of tracers in tying soil organisms into nutrient cycling; to test the depth of nutrient uptake by second growth and climax vegetation; and to describe the pathways of nutrient cycling in climax vegetation on latosols. Methods Dept of nutrient Uptake ‘two plots were established in the climax forest at EL Verte. One had a large number of young individuals of the climax forest species, and the other had nearly mature individuals whose leaves could be reached from a tower. A third plot was established in second growth where leaves could be easily reached. Six to eight similar individuals of several species were marked in each plot wherever possible. Two plants of each species received ^{32}P at 0-3 cm, two at 0.5 m, and two at 1 m. Two additional plants received no tracer (control). The rockiness of the soil prevented the introduction of ^{32}P at depths greater than 1 m. The plants were as near in height and vigor as possible, although in some cases, it was impossible to find 6 individuals of one species within the fenced area for treatment. The species used are listed in Table 1 by plots with the depth of treatment. aa ---Page Break--- Table 1. Depths, and highest counts for effective ^{32}P uptake by second growth and climax plants on Puerto Rican latosols, El Verde, Species Depth (m) Highest cpm/ae ‘Young Climax Plants Euterpe globosa 0.03 2,600 10 2,680 Guarea trichilioides 0.03 3,004 Lo" 1 Mantikere nitida 0.03 ° 1.0 and, Sloanea berteriana 0.03 ° 596 1.0 2,999 ‘Mature Climax Plants Dacryodes excelsa 0.03 387 Lo 0 us ° Mantikere nitida 0.03 157 20 99 Sloanea berteriana 0.03 309 Lo ° ‘Second Growth Plants Cecropia peltata 0.03 ° 1:0 1,389 Heliconia sp. 0.03 2,753 os 1 xo 0 Piper bias 0.08 6.57 xo 1,32. ‘Corrected for background ---Page Break--- ‘The initial level of radiation in the vegetation was sampled on all test plants using a cork borer and a rubber cork for backing. The cork borer was the same diameter as the planchet used in the beta counter so

that the geometry of the samples was kept constant. A soil auger was used to dig holes of known depth for the introduction of the isotope. A piece of Tygon tubing 2 cm 1-4. was inserted in the hole. The dosage of 32P, 6 Ci, was pre-measured in 10 ml of water in plastic bottles, so that one bottle represented 4 single doses. The isotope solution was poured into a funnel inserted in the top of the Tygon tubing and another 10 ml of plain water followed the isotope to rinse the tubing. The tubing was allowed to drain for 15 minutes before being removed from the hole. The 0.03 32P treatment

was applied by sprinkling the solution over an area after removing the litter. The large trees received 140 Ci of 32P fed at several places at the same depth in the soil. Samples of new and old leaf tissue were removed daily from the trees and adjacent vegetation using the core borer technique and counted on a beta counter for each of 20 days after the application of the isotope. The average counts per minute were expressed as cpm. In a few cases, it was possible to obtain enough fungal and root tissue and soil for 32P detection. Roots of the species tested were examined microscopically for types of mycorrhizal nutrient pathways. The second set of tests used Se, Zn, and Fe to label living plant material. Seedlings and fresh leaves were placed with their roots or petioles in 2 liters of 100 Ci of the separated isotope solution in a plastic tray with the rest of the seedling or leaf supported in an upright position by the openings of chicken wire screens (technique developed by Dr. C. Jordan). Aeration of the isotope solution facilitated nutrient uptake. The material was exposed to the isotope solution for 2 hours. In one test, the root mat with humus from the forest floor was cut into segments 6 x 3 and rolled up. The rolled root mat was wrapped in paper towels and tied with string. The roll was lowered into the aerated isotope solution (93Se or 59Fe) on chicken wire and left for 2 hours. At the end of the feeding period, the

Chicken wire was raised and the leaf bases, mat, or seedlings were allowed to drain for several hours. When the liquid had dried from the plant surfaces, the material was removed from the chicken wire using plastic gloves and was placed in marked plastic bags. The inexpensive apparatus used in feeding was disposed of at the completion of the feeding. 333, ---Page Break--- The leaves, root mat, or cut-up seedlings were taken to the field and placed over the root systems of seedlings and saplings (so 1M high) which were known to have mycorrhiza. Data were not taken by tree species, but the plots contained Nyssa glabra, Staphylea trifolia, Vantikara nitida, Suterpe globosa, and Dacryodes excelsa. For 5 months, samples of roots, soil, hyphae or rhizomorph connections, leaves and litter were collected from each plot twice monthly for counting on a 400-channel gamma counter. Samples were taken once a month beginning in September. The results were expressed as cpa/g (dry weight) of tissue. Soil samples from 1 d=) were collected once a month using a Tullgren funnel. Results and Discussion Depth of Nutrient Uptake The plants studied were not actively producing new leaves in early April, except for Decaspermum and Cephalotaxus. By late April, most of the trees had begun new growth, so that counts taken in late April for young leaf tissue showed good levels of 32P, whereas counts in early April which had to be made on older leaf tissue showed no 32P. This isotope was used because phosphorus is readily taken up by roots if the plants are physiologically active and growing. Table 1 shows that Guanes trichiliae, Heliconia sp., Piper blattera, mature Manikara nitida, and Dacryodes excelsa have shallow roots capable of taking up 32P which lies in the upper 0.03-0.06 of soil. Soil taken from 0.2 meters beneath the 1 de arena where the isotope had been applied showed no 32P. The 32P must have been bonded on soil colloids so that it was not leached downward by rain. The total rainfall for the 20 days of study was 9.1 cm in the young climax.

forest, 6.4 m deep in the near mature forest, and 20.5 cm in the second growth plot. High counts of 32P were found in soil at 0.03-0.05 M and in roots and rhizomorph tissue in all plots. Young Manilkara nitida and Sloanea berteriana absorbed 32P most efficiently from intermediate depth, 0-5 to 1.0 m (Table 1). Euterpe globosa and Piper glabrum were efficient in 32P uptake at 0.05 and 1.0 m suggesting a root system with access to a large soil volume. Cecropia peltata appeared to be deep-rooted, taking up 32P from 1.0 m only. The depth of uptake shown by these data corresponds generally with what is known about the root systems; Cecropia peltata appears to have deep, penetrating roots, and mycorrhiza have been found on this species. It is possible that indirect nutrient cycling occurs in Cecropia, some species of which are known to concentrate biologically

essential elements on poor soils (Stark, in press). Dacryodes excelsa typically forms a surface root mat and has a similar mycorrhiza, suggesting that direct nutrient cycling could occur. Fungal tissue from one meter away from the treated zones on the soil surface showed high levels of 32P 10 days after treatment. This suggests that the fungal tissue was contributing 32P, although it was impossible to establish that the fungal tissue in question was in living contact with root cells. Sloanea and Manilkara saplings were most efficient at taking up 32P from the 0.5 and 1.0 m levels in the soil. Near mature Sloanea and Manilkara were most efficient at 32P uptake from 0.03 m, suggesting that these species change in rooting habit and mode of nutrient uptake with age. Excavation showed that young Sloanea and Manilkara trees have deep roots extending into the soil. As the trees mature, they develop a surface feeder root system which appears to obtain nutrients from the litter and upper few centimeters of soil. Roots of all test plants from 0.03 m showed very high counts for 32P. Because of the irregular geometry of roots, fungi, and soils, quantitative data.

cenno be given for these parts of the ecosystem. However, detection of 32P was easy, indicating that 32P was present in all those materials. Adjacent vines and other trees took up 34P from 0.03 M only, indicating that there is an extensive intermixing of roots, especially near the surface. The techniques used for introducing the isotope can be improved by using smaller dosages of isotope at different points around the plant being studied. In one case, an isotope introduced at one point near a dicot plant root system never showed up in the leaves. The isotope may well have been introduced where there were no roots, or roots of another plant. Although the method involves some problems, it is most useful in studying rooting habit and uptake if extensive sampling is possible and if the plants are growing. The data from this study confirm the theory that Ceanothus has deep roots and takes up large volumes of soil (Stark, in press). The pathway figure shows that Fe moved quickly into the roots and leaves from labeled litter, but almost no 57Fe occurred in the soil until a month after the labeled litter was applied. The isotope moved into the humus and 0-2 cm soil about a month after the labeled litter was placed on the soil. The end of April until early June was a rainy period; even the movement of isotope by leaching was possible. Since the period was very rainy, plant growth was slow and it was not. 35 ---Page Break--- In Ceanothus, cover species of vines are known to concentrate biologically essential elements on poor soils (Stark, in press). These examples excel typifying a surface root mat and have abundant mycorrhiza, suggesting that nutrient cycling could occur. Fungal tissue from one meter away from the treated zones on the soil surface showed high levels of 32P 10 days after treatment. It suggests that the fungal tissue was contacting 32P, although it was impossible to establish that the fungal tissue in question was in living contact with root systems. Ceanothus and Mentha saplings were most efficient at taking up nutrients.

up 32P from the 0.5 and 1.0 levels in the soil. Near mature Sloanes and Hantlkara were most efficient at 2@P uptake from 0.03 My suggesting that this species changes in rooting habit and mode of nutrient uptake with age. Execution shows that your Cloanea and Nantlkars trees have deep roots going into the soil. As the trees mature, they develop a surface feeder root system which appears to obtain nutrients from the litter and upper few centimeters of soil. Roots of all test plants seem 0.03 1 showed very high count for 32P. Because of the irregular geometry of roots, fungus, and colle, quantitative data cannot be given for these parts of the ecosystem. However, detection of 32P was easy, indicating that 32P was present in all these materials. Adjacent trees and other trees took up SP from 0.05 H only, indicating that there is an extensive intermingling of roots, especially at the surfaces. The techniques used for introducing the isotope can be improved by adding smaller dosages of isotope at different points around the plant being studied. In one

case, an isotope introduced at one point near a Dityropanas morctotont never showed up in the leaves. The isotope may well have been introduced where there were no roots, or roots of another plant. Although the method involves some problems, it is most useful in studying rooting habit and 32P uptake if extensive sampling is possible and if the plants are growing. The data from this study confirm the theory that Ceeroy has deep-rooted and taprooted large volume of soil (etark, dn presse Yutetent). Figure 1 shows that 59Fe moves quickly into the roots and leaves from labelled litter, but almost no 59Fe occurred in the soil until a month after the labelled litter was applied. The isotope moved into the arms and 0-: cm soil about a month after the labelled litter was placed on the soil. The end of April until early June was a rainy period when the movement of isotopes by leaching was possible. Since the period was very rainy, fungus growth was slow and it was not 335 ---Page Break---

Fig 1. Monthly or bimonthly radiation level in soil, water, roots, and 0-3 cm soil in plot treated with °F labeled at Verde, Puerto Rico. Fig. 2. Monthly or bimonthly radiation level in leaves, roots, and 0-3 cm soil in plot treated with 8R labeled as habitat at Hl Verde, Puerto Rico. ‘No. 89Fe was found 10 cm in the soil Mat 136 ---Page Break--- Possible to find rhizomorphic tissue for counting. Because no Fe occurred in the soil for over a month, the isotope must have entered the leaves from the organic litter, but because rhizomorphic tissue was not present in quantities suitable for counting, there is no proof that direct nutrient uptake took place. The data show that 59Fe moved into the roots and leaves, but they do not show what pathway was taken, i.e., free-living bacteria, soil animals, or mycorrhiza. Heavy rain may have leached enough 59Fe from the dead litter so that the roots had access to surface water with 59Fe. The level of 59Fe in roots and leaves decreased after the first month, while the 59Fe content of the soil increased slightly through mid-July. The humus increased in the soil for several months as the isotope was released from the litter, and then gradually decreased. The increase in 59Fe in the humus during July and August is probably the result of a concentration of the isotope from the decomposition of carbohydrates (i.e. loss of organic matter and conversion of litter to humus). The litter showed a reduction while the humus increased slightly in activity suggesting the conversion of litter to humus. Because the leaves did not increase in 59Fe after the first month, we can conclude that little 59Fe was transported from the roots to the leaves, and that the roots were not transporting 59Fe from the litter, soil, or humus in significant quantities. The leaves were not growing during this time and new growth did not appear, except for a small amount in mid-June, which may explain the failure of the leaves to take up more Fe. It is significant that Fe never appeared at 15 cm in the soil in

Gotober as well as in the companion tests, indicating that this soil is efficient at bonding and holding 59Fe against leaching. The isotope was not moved into old leaves in significant amounts. The pattern of 59Fe movement from the labelled humus-root mat was very similar to that from labelled litter except that the young leaves and roots showed a marked increase in mid-June in the most tested (Figure 2). This increase coincides with periods of heavy rains, although the rain may not explain the root behavior. Since the movement of 59Fe out of the humus-root mat and out of litter was not obviously different, we can assume that this isotope moves from both media to roots via similar pathways. The data suggest that roots can obtain 59Fe more readily from the humus mat than from litter, which defines a pathway of nutrient cycling involving free-living fungi, bacteria, and animals rather than mycorrhiza. Young leaves showed a high level of 59Se in early May when new leaves were appearing, but older leaves never showed significant levels of 59Se in the litter plot (Figure 3). The young leaves ... ---Page Break --- ... Figure 3- Monthly or bimonthly radiation levels under 0 cm soil plots treated with 786 labelled humus-root mat. Upper scale represents the change in the ... Figure ... Monthly or bimonthly radiation levels in seedling leaves, root, and 0 cm soil plots

treated with 75S labelled humus-root mat at El Verde, Puerto Rico. The top scale represents the radiation level of the humus-root mat ... ---Page Break --- ... showed a second increase in 59Se in mid-June as with Fe (mat). These phenomena, like August, not in ‘explanation’ for this. The roots of the seedlings increased in 59Se during the first month, and then decreased markedly. From July 7 onward, they increased in the level of 59Se again. This fluctuation could result from either sampling error or some phenomenon of root metabolism; it is possible that the isotope was released from litter and then taken up in pulses since similar fluctuations occurred in the Fe studies. The ...

level of T58e gradually increase! wi =: su In the soil, but no significant amount of isotope reacted 15 cx depth in the soil. The Iams increase? in the amount <P iste) vic the litter tend to decrease in radioactivity, ay would be yresistel, Unfortunately, It is difficult to get a tnitor: labeling in litter co that minor fluctuations may be due to initial differences in level of labeling, in spite of subsampling. Sot} animals collected in early June and August showed high levels of 75Se suggesting that they were very important in breaking down litter in this habitat. E°') sunset were high in T58e, although there was no way of ascertaining whether these Sunci were free-living or mycorrhizal. The results from the 75Se tests suggest that this lectope moved from the litter to soil fungi and soil animals in the upper soil layer (0-3 cm) and that uptake occurs in this layer (=? om and humic). Nothing can be said about uptake of isotope by deep roots because the isotope did not move into the r soil which is a heavy clay with restricted drainage. Each level of Tce in the roots during August-Nov. must have come from the huts or soil since the litter had almost no Tse. This pattern of nutritional movement of isotopes was found for tritium in these sites (¢ine and Jenin L96E). Inmen T5se was applied in the humus-root but, almost no isotope appeared in either the young crop venes (igs aly The roots and 0-3 cm soil increases in Tie at much the same rate, with more radioactivity entering the soil in the first two months than occurred with Inbelle? litter, Tala eusseute a leaching of TSE from the humus-root mat by rain. Previously, it was thought that much uptake of nutrients occurred in this hue layer, although these data only partly support that view for the month of April through November. Since the root and soil became heavily shelled at the green vine (nia- June and early September), this suggests that uptake of (8 was from the 0-3 cm soil or the mat indirectly and not from litter in this case. Since the mat was already pasty

lesnyed, the release of materials into the soil was more rapid than with litter. The study was complicated by the fact that the seedlings and canopy were small and heavily shaded ---Page Break--- so that they were not able to put on septa growth. Even when the isotope was applied in the humus-rich mat, no isotope appeared at 15.23. In September, the roots in the mat and uptake by the roots (Fig. 4). None of the control leaves, litter or soft showed significant levels of DFe, tse, zn. The 652n tests were designed to get around the problems of slow growth. The plants well in this test were 8 species of local tree seedlings planted in poor sand with a surface organic layer. The seedlings were under 5 cm high and were grown in plastic-lined galvanized tanks in sandy-shale. These plants showed the same initial increase in 652n in the leaves during the first month after application of the labelled litter as did the 95e and 09Pe tests (Fig. 5). The roots of the seedlings and the 0-3 cm soil both increased slightly in 652n for two months, and then decreased. By August 1, there was considerable loss in the 0-3 cm soil but little in the roots. Isotope appeared in the first few months, so that it could not be measured. The litter gradually decreased in 652n, the isotope 652n was applied to plant surfaces as well as taken up internally. I found that leaves, roots, and soil in plots treated with externally applied 652n were higher in this element than were those in plots where it was applied internally. The pattern persisted throughout the tests. Apparently 652n can be leached from plant surfaces and is then available for uptake, while leaching of internal 652n appeared to be insignificant. Since zinc is needed in small amounts by plants, and since it is poorly

transported, it is not unusual that it did not occur in the leaves in great quantity. Roots normally concentrate zinc, and it is surprising that zinc did not become more abundant in the roots than it did. The roots showed a slight increase in 652n on

September 8 Following the high levels of this isotope in the soil. Sampling in rail containers tends to disturb the roots and may well do serious harm to nutrient cycling pathways. ‘The seedlings did not put on as much new growth as was expected. This technique of studying nutrient cycling requires that the scientist be continually resident in the field. Since this was not possible in the present study, some information was lost. Every modification of Heather and every change in plant metal can affect the ultimate results of this type of study. Some of the variability in this study resulting from sampling error can be overcome by wider sampling and more compositing of samples. One major problem which should be studied is the effect of physiological activity of the plants on isotope uptake. Both of the also ---Page Break --- Fig. 5.1 Monthly or bi-monthly radiation levels in seedling leaves, litter, roots, and 0-3 cm soil for plots treated with Zn, yielded litter at El Verde, Puerto Rico. ---Page Break --- Studies reported here were limited by the failure of the plants to grow. Studies are needed which determine whether photosynthesis, root metabolism, or the rate of movement of the transpiration stream, or some other physiological process will best coincide with isotope uptake. The behavior of different physiological conditions of the tree would be helpful in defining which isotope to use and when. Unfortunately, most of the studies on isotope uptake have used rapidly growing greenhouse plants or temperate plants during the growing season. ‘The periodicity of growth in the tropics is not well understood. Acknowledgements ‘The author is grateful to the Atlantic Energy Commission for making this study possible and for the cooperation and assistance of personnel from the Puerto Rico Nuclear Center. Literature Cited Kine, J., and C.F. Jordan, 1968. Tectonic movement in the soil of the tropical rainforest, “Soil 160: 550-551. Stark, H, 1969. Nutrient cycling in the Amazonian Rain Forest. In press. Went, P.W., and M.I. Stark.

19684. Mycorrhiza. BioScience 18 (21): 4035-1039. Went, F.W., and M. Stark, 1968. The biological and mechanical role of soil fungi. Proc. of Nat. Acad. of Sci. 69 (2): 197-205. The studies reported here were limited by the failure of the plants to grow. Studies are needed which determine whether photosynthesis, root metabolism, or the rate of movement of the transpiration stream, or some other physiological process will best coincide with isotope uptake. The behavior of different physiological conditions of the tree would be helpful in defining which isotope to use and when. Unfortunately, most of the studies on isotope uptake have used rapidly growing greenhouse plants or temperate plants during the growing season. The periodicity of growth in the tropics is not well understood. Acknowledgments The author is grateful to the Atomic Energy Commission for making this study possible and for the cooperation and assistance of personnel from the Puerto Rico Nuclear Center. Literature cited Kine, J., and C.F. Jordan, 1968, Tritium movement in the soils of the tropical rainforest, Soil 160: 550-551. Stark, H., 1969, Nutrient cycling in the Amazonian Rain Forest. In press. Went, F.W., and M. Stark, 1968, Mycorrhiza. BioScience 18 (21): 1035-1039. Went, F.W., and H. Stark, 1968, The biological and mechanical role of soil fungi. Proc. of Nat. Acad. of Sci. 60 (2): 197-205.