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ECOLOGY OF THE LEAF LITTER HERPETOFAUNA OF A NEOTROPICAL RAIN FOREST: LA SELVA, COSTA RICA

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RESUMEN

Durante un período de 13 meses consecutivos se estudió la herpetofauna de hojarasca en relación con sus hábitos alimenticios y ambiente físico y estructural en un área de bosque tropical perennifolio no perturbado y en una plantación de cacao adyacente y abandonada 20 años atrás, ambas localizadas en la estación biológica La Selva, Costa Rica. El cacaotal se considera como un ambiente perturbado debido a la introducción de un agrosistema.

Se midieron 44 variables ambientales, encontrándose para la mayoría diferencias entre el bosque y el cacaotal, entre parcelas de muestreo diurno y nocturno, y entre los diferentes meses. Por ejemplo, la precipitación, el volumen y profundidad de la hojarasca el volumen y profundidad de la hojarasca la cobertura de herbáceas y la humedad muestran variaciones estacionales. En el bosque existen más palmas, troncos, árboles con contrafuertes, árboles jóvenes y lianas que en el cacaotal. En comparación con el bosque, la capa de hojarasca es más profunda en el cacaotal, el cual además carece de un sotobosque bien definido. En términos de parámetros ambientales se concluye que el cacaotal es un habitat más variable y menos predecible que el bosque, lo cual no necesariamente implica que sea más inhóspito o severo.

Se colectaron 1967 individuos de 47 especies de anfibios y reptiles. Se encontraron diferencias entre el número de especies e individuos del bosque y del cacaotal, las parcelas diurnas y nocturnas y los 13 meses. El mayor número de especies se encontró en el bosque, en el cual tuvo también la mayor diversidad. En el cacaotal se registraron los valores más altos de abundancia, densidad por parcela y dominancia. En este ambiente también se registraron los mayores valores de número total de individuos, agregación y densidad para las 5 especies más abundantes. El grado de dominancia encontrado en estos ambientes de bosque y cacaotal es mucho mayor que el conocido para los ecosistemas tropicales de hojarasca del Viejo Mundo. El número total de especies y de individuo, así como el número total de individuos de las especies principales si-

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guen un marcado patrón estacional, alcanzando valores mayores hacia el final de la época seca en coincidencia con valores máximos de las poblaciones de artrópodos y de la profundidad de la capa de hojarasca.

Los artrópodos como recurso alimentario están repartidos entre las especies de la herpetofauna. Al comparar los contenidos estomacales con la abundancia de presas (obtenida con trampas de bote) se observó que algunas especies consumen los artrópodos proporcionalmente a su disponibilidad en la hojarasca. Algunas especies consumen presas pequeñas, principalmente ácaros y hormigas de cuerpo duro, mientras que otras consumen presas de mayor talla y cuerpo blando. Algunos de los especialistas, como *Dendrobates pumilio,* consumen hormigas de talla pequeña y en gran cantidad. Otros, como *Gastrophryne pictiventris,* en cambio consumen hormigas de gran tamaño y en cantidad reducida. Se discuten en detalle las dietas de las especies principales.

Eleutherodactylus bransfordii y *D. pumilio,* las dos especies más abundantes, se distribuyen más densa y agregadamente en el cacaotal que en el bosque y tienen dietas diferentes: *E. bransfordii* consume pocas presas grandes en proporción similar a la de su disponibilidad, mientras que *D. pumilio* consume solamente ácaros y homigas pequeñas. Establezco como hipótesis: (i) que estas 2 especies son más existosas en ambientes perturbados e impredecibles, y (ii) que al inicio del abandono del cacaotal eran más dominantes pero con el trancurso del tiempo sus poblaciones en bosque y cacaotal alcanzarán la igualdad. Se requiere de estudios adicionales para determinar los factores limitantes de las poblaciones de estas 2 especies, uno de los cuales probablemente sea la competencia con otras especies aunque no hay evidencias para apoyar esta idea. Propongo que las poblaciones de *E. bransfordii* están limitadas por depredación. Las poblaciones de *D. pumilio*, especie que contiene alcaloides tóxicos en la piel y no es preferida por los depredadores, pueden estar limitadas durante el período larvario debido a depredación y/o competencia.

Estas diferencias entre el bosque y el cacaotal así como la marcada estacionalidad tanto para la hepetofauna como para varios parámetros ambientales, aún más marcada en el cacaotal, sugieren la necesidad de continuar con estudios sobre la estacionalidad de los trópicos con fines teóricos y prácticos. Propongo que la creciente destrucción de los trópicos propiciará cambios estacionales cada vez más pronunciados, lo cual debe ser entendido y considerado en cualquier intento de manejo de los trópicos o del estudio teórico sobre la sucesión tropical.

ABSTRACT

This study utilized numerous multivariate and other statistical techniques in an ecological analysis of the leaf litter herpetofauna of a neotropical rain forest, at La Selva, Costa Rica. Leaf-litter plots for thirteen months were studied both during the day and at night, in an undisturbed forest and in an adjacent fallow cacao plantation. At each litter plot, the herpetofauna were collected and over fifty environmental parameters were measured. The forty-seven species of amphibians and reptiles collected showed both a high degree of dominance and high diversity. The diets of these species were studied using stomach content analyses. For the herpetofauna, their diets, and the environmental parameters, the presence and degree of diel and seasonal differences, and the differences between the undisturbed and disturbed habitats, were analyzed. Significant seasonality was found for both the herpetofaunal species and the environmental parameters. Significant differences were also found between the forest and cacao habitats. The disturbed cacao habitat had fewer species, a higher overall abundance, lower diversity, greater patchiness, and greater seasonality.

INTRODUCTION

The most complex and diverse terrestrial ecosystems are in the tropics. Among these the lowland evergreen rain forests have the highest species diversity, biomass per unit area, productivity per unit time, and complexity of species interactions. The maintenance and derivation of the diversity in these forests remain among the most intriguing problems in evolutionary and ecological biology. This study addresses the folowing questions:

(1) For a large number of environmental variables, what differences are there between un undisturbed forest and adjacent disturbed, fallow cacao forest? (2) What differences are there between the numbers of individuals or species collected in the forest and the cacao? (3) What differences are there between the numbers of individuals or species collected at night and during the day? (4) Is there any seasonality in this system, either for the environmental variables, the species, or in their diets? (5) I will provide autecological data on the most abundant species, and discuss interactions between them.

MATERIALS AND METHODS

The study area was Finca La Selva, Heredia Province, Costa Rica. This area is in a lowland, evrgreen west forest (Holdridge, 1967) at an altitude of 60 m, with a mean annual rainfall of 3969 mm. Two dry months, January and February, usually have an average of less than 200 mm rainfall, while the wet months of March-December have an average of more than 200 mm rainfall. The study was carried out at two sites: one in a relatively undisturbed forest and the other in an immediately adjacent plantation that was once planted with cacao trees *(Theobroma cacao)* but has been fallow for at least 20 years. I consider the old cacao plantation as a disturbed ecosystem. Data were collected both at night and during the day over a period of 13 consecutive months, from December, 1972 to December, 1973.

LITTERPLOTS

Ninety 8 x 8 meter plots were sampled in the leaf litter over the thirteen month period, using a random selection process from a grid of plot locations in each forest. The 90 plots are divided into forest-day (30), cacao-day (21), forest-night (27) and cacao-night (12). There was a four day sampling period each month. Plots of this size and type have been used both in the New World and Old World tropics to assess amphibian and reptile populations (Scott, 1976; Lloyd et al, 1968; Toft, 1980; Inger and Colwell, 1977). An 8 x 8 meter quadrat was marked off with string by 2-4 persons. The location of the plot was based on the coordinates of the plot within the grid. Environmental variables were measured both prior to and after the collection of animals. The collectors moved inward from the boundaries of the plot, moved all litter material that they encountered, and placed all amphibians and reptiles in collecting bags. Fleeing animals tend to move towards the center, where there is the highest probability of capturing them. This method is known to disproportionately undercount snake populations, (Inger, 1980a; 1980b; Carl Lieb, pers. comm.) as snakes can detect the investigators and flee. Each of the specimens collected was identified to species; snout-vent length was measured, and the specimens were tagged and preserved for later studies.

Environmental Variables

1. Number of buttress trees in each plot
2. Buttress cover: percent of the ground covered by buttress trees

3. Buttress diameter: Mean diameter of buttress trees in the plot (cm)
4. Big tree number: Number of large trees, excluding buttresses
5. Big tree diameter: Mean diameter of large trees (cm)
6. Number of palms in each plot
7. Number of saplings in each plot
8. Number of logs in the litter
9. Log cover: Percent of the ground covered by logs
10. Log diameter: Mean diameter of logs found within the plot (cm),
11. Number of lianes in each plot
12. Herb cover: Percent of the ground covered by herbaceous vegetation
13. Measured depth: Actual litter depth (cm)
14. Leaf depth: Number of leaves pierced by a stiff wire (average of 5)
15. Ranked depth: Qualitative rank of litter depth (0–5)
16. Burlese volume: Volume of 1 x 1 m^2 portion of the leaf litter, from a corner of the 8 x 8 m plot
17. Ranked debris: Qualitative rank of amount of litter debris (0–5)

Except for litter depth variables and Burlese volume, all of the above variables were measured after the litter plot was completed. The following 24 climatological variables were measured at both the onset (–1) and completion (–2) of the sampling, and the average (–ave) of the two and the difference between them (–diff) were calculated:

1. Air temperature–1
2. Air temperature–2
3. Air temperature–ave
4. Air temperature-diff
5. Substrate temperature–1

6. Substrate temperature–2
7. Substrate temperature–ave
8. Substrate temperature–diff

To measure temperature (^{O}C), a fast reading thermometer was used.

9. Wet bulb–1
10. Wet bulb–2
11. Wet bulb–ave
12. Dry bulb–1
13. Dry bulb–2
14. Dry bulb–ave

Wet and dry bulb readings were obtained from a sling psychrometer.

15. Humidity–1
16. Humidity–2
17. Humidity–ave
18. Humidity–diff

Humidity was measured by a hygrometer.

19. Weather: (1–5) 1: clear; 2: sunny; 3: cloudy; 4: overcast; 5: rain
20. Rainfall-today: rainfall the day the given litter plot was sampled (mm)
21. Rainfall-sampling: rainfall for the entire 4 day sampling period (mm)
22. Rainfall-3 prior: rainfall 3 days prior to the sampling period (mm)
23. Rainfall-total: total monthly rainfall (mm)
24. Rainfall-average: average daily rainfall for that month (mm)

Rainfall data are from the La Selva Field Station Climatological Report. In addition to the aforementioned variables, the following 3 miscellaneous variables were recorded: Slope, Plot number (1–90), and Starting time (time of day at the start of the litter plot).

Stomach Contents

With the exception of the snakes, stomach content data were obtained for all amphibians and reptiles in the 90 plots. For the rarer species, stomach contents were obtained for all the individuals collected; sub-samples were taken for the abundant species.

The snout-vent length was recorded for each individual, the stomach was removed, and the length, width and depth of each stomach measured (mm). Invertebrates were classified to the level of order in most cases. Hymenopterans were further classified as either ants or all others. Larvae were classified as Diptera, Lepidoptera, Coleoptera, and unidentifiable. Arachnids were classified as spiders, mites and others. The only crustaceans were Isopoda. The classes Diplopoda and Chilopoda were put into one group, the "Centipedes". The length and width of each prey item were measured. Other studies (Pianka, 1973) have used volumetric displacement to determine prey volume, but this was deemed impossible with the very small prey sizes found in frogs and lizards. Prey length and width were multiplied to get an estimate of prey size in two dimensions. This allows a comparison between individuals of a more precise nature than prey numbers alone. For each individual, the following were determined for each prey category: number of prey, percent of the total number of prey in the stomach, area of each prey group, percent of the total area of prey in the stomach, and average prey length for that prey group. The following were determined for each species, for each prey category: mean number of each prey per individual, maximum number per individual, mean prey length, maximum prey length, mean percent of total prey area, and maximum percent of total prey area. All of the above were determined for the 90 plots, and for the forest and cacao separately.

Data Analysis

Data were analyzed using the IBM 370 at the University of Southern California. Programs used included those in SAS

(Statistical Analysis System), and EAP (Ecological Analysis Package). The following univariate and multivariate statistical analyses were used: Student's t-test, Pearson product-moment correlation, Multiple Analysis of Variance, Cluster Analysis, and Multiple Discriminant Analysis. The condition of homoscedasticity was met, precluding any necessity for non-parametric statistics. In the analysis of variance, an adjustment for unequal sample sizes was used.

Cluster Analysis is used to classify OTU's (in this case species and/or sites) into discreet sets, based on a similarity matrix (Pimentel, 1976). The distance index chosen is the Bray-Curtis index (Clifford, 1975; Smith. 1976), also called the Czekanowski index (Smith, 1976; Hall, 1969; Goodall, 1973). This is a commonly used distance index in ecological surveys (Smith, 1976). It is the index of preference for species data, because double-zero comparisons have no effect on the distances (Orloci, 1973; Smith, 1976). The Bray-Curtis index has been shown to express changes in the species composition of a system over time better than any of the other commonly used indices (Canberra, Renkonen's, Pearson's, etc.) (Huhta, 1979). Agglomerative hierarchical classification was performed to display, using a two-dimensional dendrogram, the relationships between the entities (either the sites or the species).

Multiple Discriminant Analysis, or canonical variates analysis (Smith, 1976; Hope, 1969) is used to study the relationships between predetermined groups of entities and a set of attributes or variables measured with those entities. Discriminant analysis has been used extensively in ecological research to determine major resource axes, assess niche metrics, and evaluate resource dimensions and utilizations (Day, 1971; Dueser, 1979; Gray, 1979; Green, 1971; Holmes, 1979; Hudson, 1976).

RESULTS AND DISCUSSION

Sites and Environmental Variables

Some environmental factors, such as humidity, air and substrate temperature, and wet and dry bulb, vary little among the 90 litter plots, and have small variances. Others, such as number of species, number of individuals, buttress and big tree diameters, and herb, log, and buttress cover, are quite variable.

The histograms (Figures 1-2) depict the distributions of the variables among the sites. The number of species has a roughly normal distribution, but the number of individuals (herp number) does not. The number of palms per plot ranges from 0 to 25, but all plots with more than 4 palms are in the forest and not the cacao. The mean depth of the leaf litter is greater in the cacao than the forest, but there is more debris on the ground in the undisturbed forest than in the cacao.

Pearson product-moment correlation coefficients were computed between the variables. All temperature and humidity variables measured both at the start and end of each plot were highly correlated ($p<.001$). The Burlese volume is strongly correlated with air and substrate temperature, and wet and dry bulb ($p<.01$), but the actual litter depth is less so ($p<.05$). Litter depth (both rank and actual measurements) has a significant positive correlation ($p<.01$) with the numbers of amphibians and reptiles. The number of palms has a high negative correlation with the numbers of individual amphibians and reptiles, yet a positive correlation with the number of species. In those plots with more large trees there is deeper litter, and a greater litter volume.

The number of environmental variables was reduced to 28 on the basis of high intercorrelations (Table 1). The actual measured litter depth values were retained; it was originally thought that there might be too much variability using the actual depth rather than a ranking, but this was not the case.

Both rainfall during the sampling period and the total monthly rainfall begin to increase in May and peak in July (Table 1; Figure 3). This rainy season from April to September is characteristic of the Central American tropics (Wolda, 1979; Scott, 1976), as is the increase in rainfall again around November-December. The pattern at La Selva for the year of this study is consistent with other years (Savage, pers. comm.), with other Central American lowland tropical sites for both the same year (Wolda, 1978; 1979) and for other years, and with some Old World tropical sites as well (Inger, 1980a; 1980b). The rainfall patterns in this study period are typical for tropical lowland wet forests (Holdridge, 1967). Any evidence of seasonality as a response to rainfall has implications not just for La Selva, but for tropical ecosystems in general. I use season to refer to a period in the year with a specified and predictable kind of weather pat-

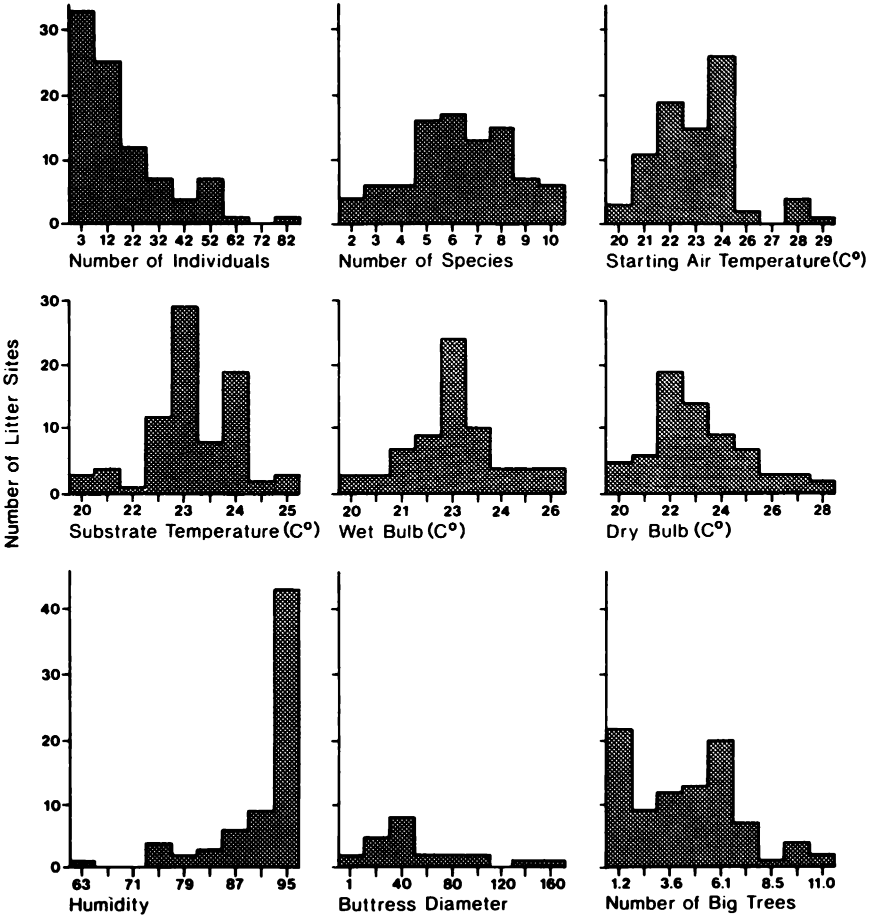
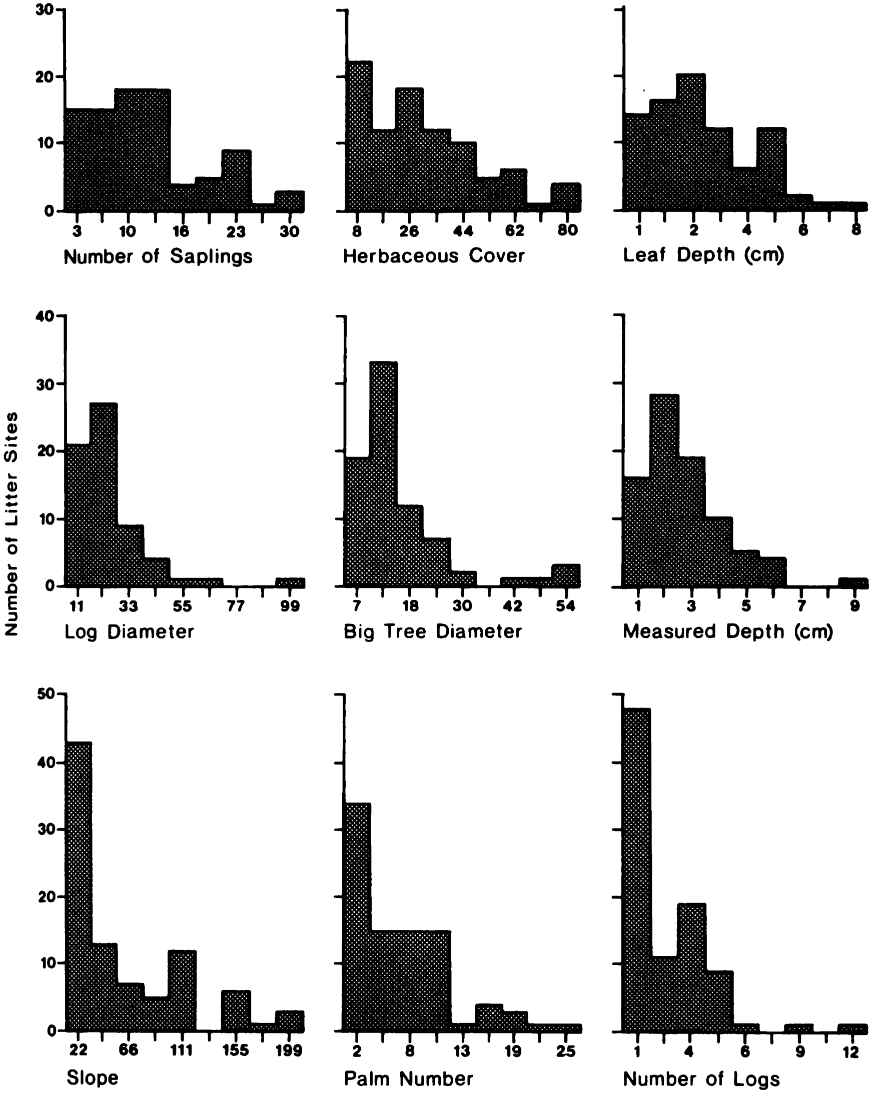


Figure 1

Histograms of Variables: Distribution of 22 variables over the 90 litter plots.



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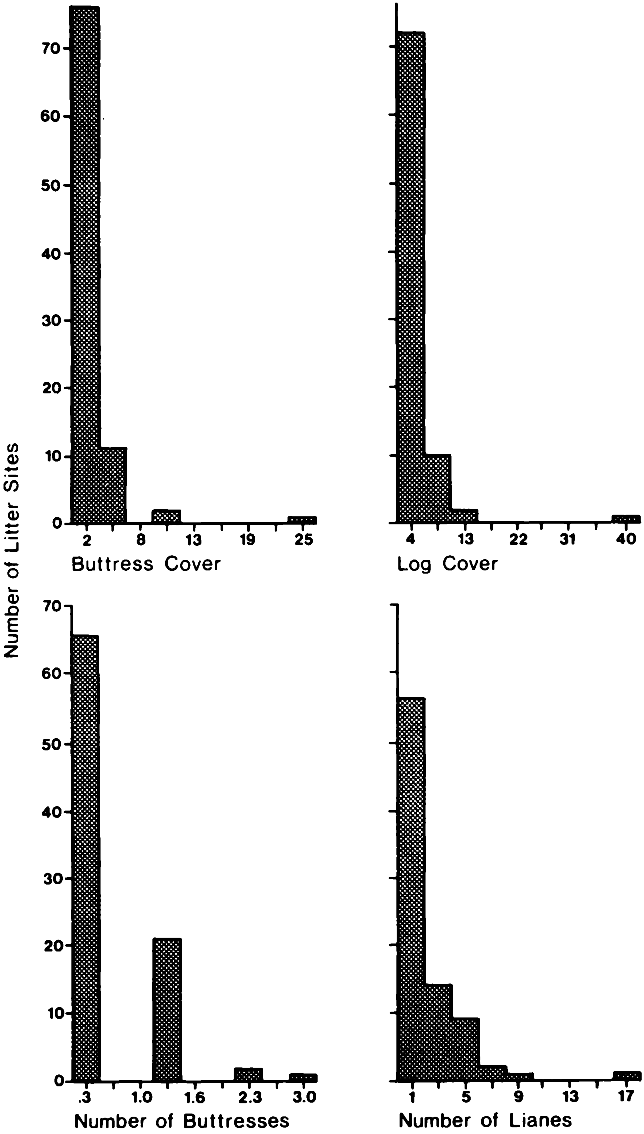

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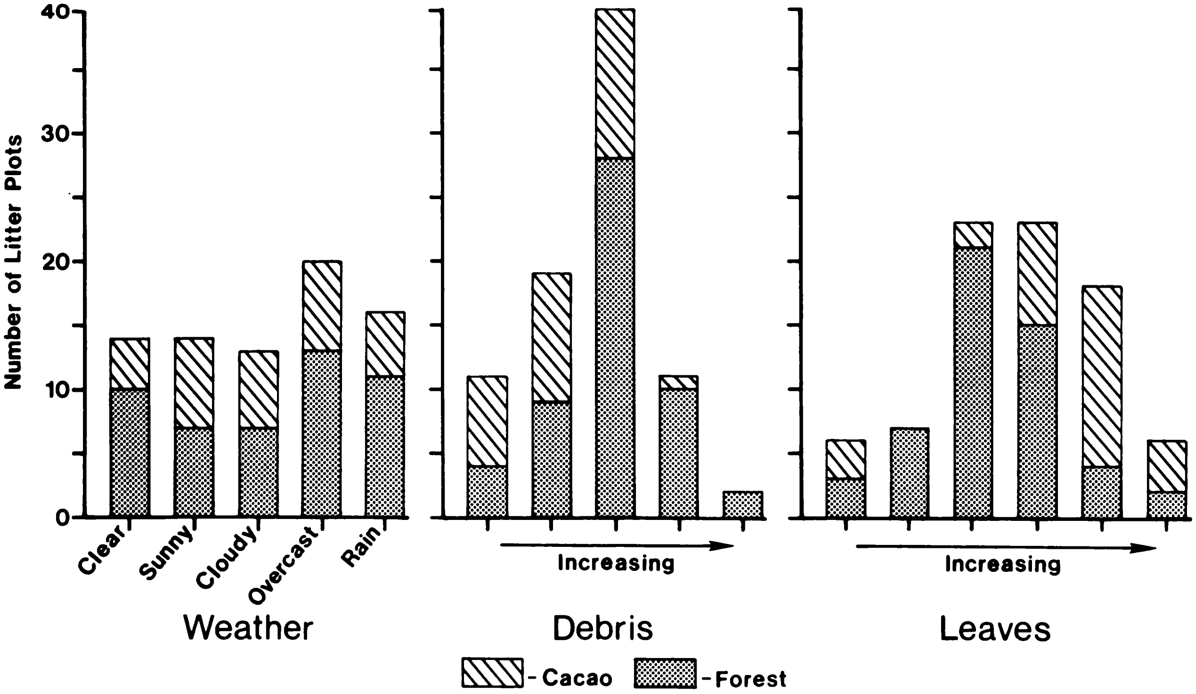

Figure 2

Histograms of Variables: Distribution of weather, debris, and leaves over the 90 litter plots. Separated into forest and cacao plots.

Table 1

Monthly Averages of Environmental Variables:
December, 1974-December, 1975

MONTHLY AVERAGES

Variables	Dec1	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec2
Herp Number	19.3	15.7	36.7	33.5	32.8	33.0	27.0	24.0	11.3	14.3	14.5	15.2	24.6
Herp spp.	6.7	5.7	7.5	8.3	8.0	6.8	6.8	7.0	4.9	5.3	4.7	5.5	6.0
Buttress Number	0.3	0.8	0.0	0.3	0.2	0.1	0.2	0.2	0.1	0.7	0.2	0.7	0.3
Buttress Cover	0.2	2.2	0.0	4.5	0.5	0.3	0.3	0.5	0.2	2.2	0.5	3.2	0.8
Buttress Diameter	–	38.3	–	97.5	50.0	20.0	70.0	60.0	27.5	53.8	50.0	96.3	75.0
Big Trees Number	2.0	2.3	4.8	3.0	4.7	6.5	4.5	4.5	6.9	2.0	22.2	2.5	3.0
Big Tree Diameter	–	18.2	18.2	19.5	12.0	19.4	16.6	12.2	25.9	15.3	22.5	15.0	21.6
Palms number	2.3	5.9	7.7	5.2	3.8	6.1	6.2	5.7	3.3	8.0	8.2	6.8	5.5
Saplings Number	10.3	9.8	13.8	6.8	13.8	4.4	9.2	8.5	7.9	10.3	15.2	11.7	13.8
Log Number	1.8	3.2	2.7	3.0	2.7	1.1	2.2	1.7	0.4	1.5	1.2	2.2	1.1
Log Cover	1.6	1.3	1.5	10.5	2.0	1.7	1.5	3.8	0.9	1.8	1.2	0.8	1.0
Log Diameter	20.3	11.6	8.8	12.8	14.5	22.5	15.8	24.2	14.7	47.8	18.3	14.8	16.0
Lianes Number	–	1.2	0.7	1.0	2.8	1.8	1.8	1.7	1.3	1.7	1.0	3.8	1.1
Herb Cover	16.7	26.5	30.8	37.5	41.7	26.3	37.5	26.7	23.0	34.2	18.3	13.8	14.0
Slope	60.8	14.5	89.2	52.5	68.3	31.3	42.5	43.3	15.2	21.7	53.3	85.0	73.1
Depth: Measured	–	2.0	2.7	1.9	2.1	4.0	2.2	1.9	3.7	1.3	1.1	1.4	1.6
Burlese Volume	8.3	10.0	9.0	15.2	16.0	31.1	15.5	11.5	0.0	7.0	7.0	9.2	9.6
Air Temperature- Diff.	0.1	0.04	0.4	–0.5	0.4	0.2	0.0	0.0	–0.2	0.2	–0.07	–0.6	–0.1
Rainfall-Sampling Period	67.8	128.8	9.8	25.8	0.0	39.1	83.3	189.4	186.8	38.7	55.8	58.7	23.6
Rainfall-Total Monthly	261.1	256.4	184.8	116.2	168.7	256.0	428.1	542.0	402.4	187.6	319.2	340.2	299.8

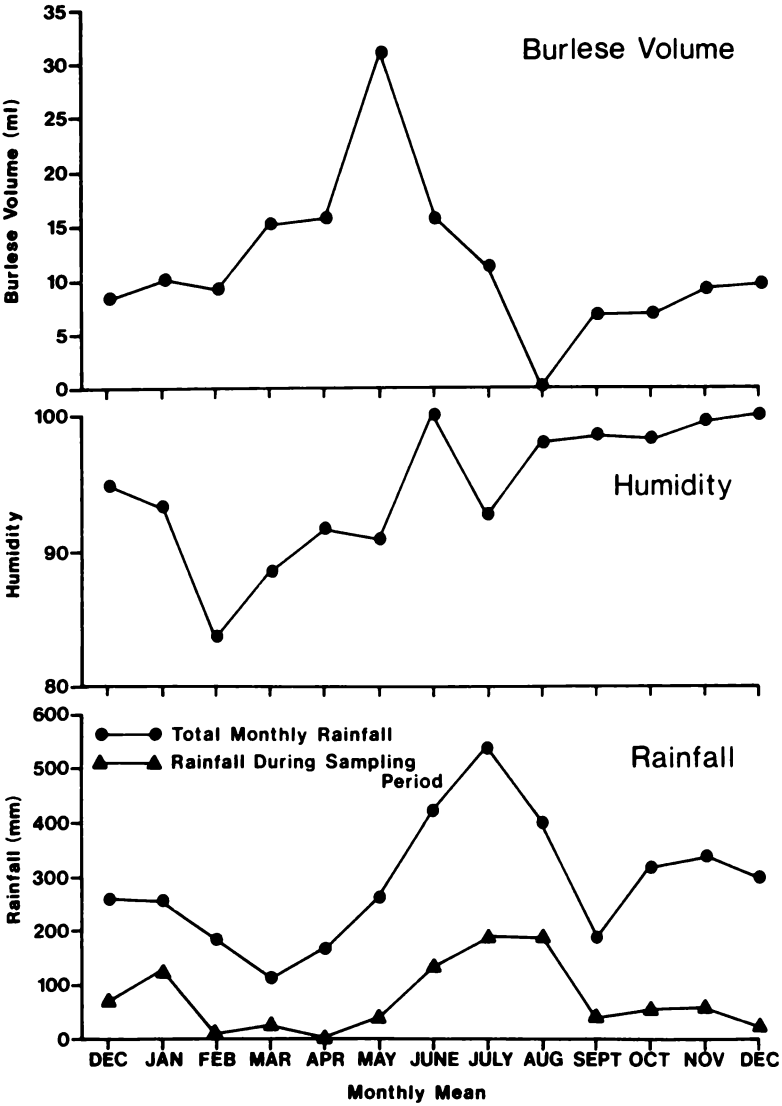

Figure 3

Seasonal patterns of major variables. Monthly mean Burlese volume, humidity, rainfall, number of saplings, herbaceous cover and litter depth.

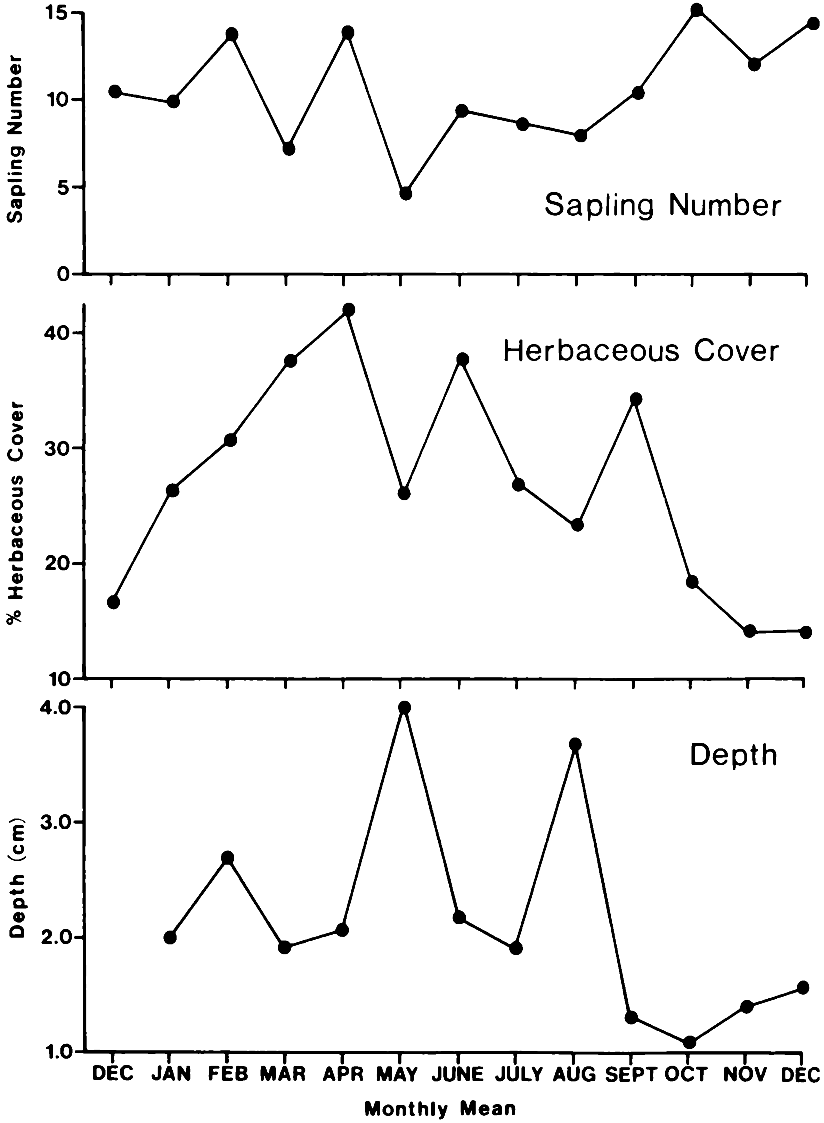

Figure 3 (continued).

tern. In this case, it refers to the rainy and dry seasons. Seasonality refers to a response by environmental factors and/or animal populations to these seasons.

There is a seasonal pattern to the volume of the leaf litter (Figure 3). The peak Burlese volume is in May, during the onset of the rainy season. Towards the end of the rainy season, in early August, when rainfall is still relatively high, the volume of the leaf litter is at its lowest, and begins to increase shortly thereafter. During the driest months of the year, when the trees lose more leaves, the turnover is slow enough to allow some litter to accumulate (Lloyd et al, 1968). This pattern is less apparent for actual measured depth (Figure 3), which is more variable. The shallowest litter is found just at the end of the rainy season, in September. Herbaceous cover is also somewhat seasonal, with a slow increase during the dry season, from a minimum in November to a maximum in November to a maximum in April. Humidity varies between the months (Figure 3), with a gradual rise from a low in February to a high in December.

A t-test was used to test for differences between the means of the environmental variables in the forest and the cacao, and between plots done at night and those during the day. The two variables with significant differences between night and day at the .01 level are: Herp spp ($p<.001$) and Humidity-1 ($p<.01$). There are significantly more species of amphibians and reptiles collected at night than during the day. This may be influenced by greater ease of capture of diurnal species at night. Humidity is significantly greater at night, even though there is no significant difference in temperature.

The variables that have a highly significant forest-cacao effect ($p<.0001$) are listed below, as well as whether the value of the variable is greater in the forest (F) or in the cacao (C): Number of individuals (C), Number of frogs (C), Big tree diameter (C), Number of palms (F), Number of logs (F), Log cover (F), and Number of lianes (F). The following variables have a significant ($p<.05$) forest-cacao effect: Air temperature (C), Buttress number (F), Leaf depth (C), Ranked depth (C), Measured depth (C), Herp spp (F), Log diameter (F), Saplings (F), and Slope (F).

Amphibians and reptiles are therefore significantly more abundant in the cacao than in the forest. There are more palms, logs, lianes, and saplings in the forest than in the cacao.

Table 2

Multigroup Discriminant Function Analysis, with 13 months of the study used as a priori groups. Three part table: one-way anova for each variable, latent roots and significance test for each axis, and coefficients of determination for the variables constituting the axes.

MULTIGROUP DICRIMINANT FUNCTION ANALYSIS
Groups = 13 months

One-Way Anova for Each Variable

Variable	F
Herp Number	0.49
Herp spp.	2.43
Buttress Number	1.57
Buttress Cover	1.26
Buttress Diameter	1.36
Big Trees Number	5.49*
Big Tree Diameter	0.96
Palms Number	0.68
Saplings Number	1.47
Logs Number	1.56
Log Cover	2.27
Log Diameter	2.00
Lianes Number	0.75
Herb Cover	1.32
Slope	1.66
Depth: Measured	3.88*
Burlese Volume	9.76*
Humidity-1	4.72*
Air Temperature-1	5.17*
Starting Time	0.40
Rainfall: Today	6.65*

*: significant F ($p<.05$)

Table 2 (continued)

Latent Roots & Significance Test for Each Axis

Axis	Root	%	Cumulative %	Chi Squared	d.f.
1	6.32	35.7	35.7	141.33*	34
2	3.90	22.1	57.8	112.83*	32
3	2.29	12.9	70.7	84.49*	30
4	2.01	11.4	82.1	78.34*	28
5	1.17	6.6	88.8	55.11*	26
6	0.62	3.5	92.3	34.25	24
7	0.43	2.5	94.7	25.60	22
8	0.41	2.3	97.0	24.41	20
9	0.23	1.3	98.3	14.66	18
10	0.18	1.0	99.3	11.53	16
11	0.08	0.4	99.8	5.42	14
12	0.04	0.2	100.0	2.63	12

* designates a significant axis ($p < .05$)

VARIABLES CONSTITUTING AXES: COEFFICIENTS OF SEPARATE DETERMINATION

Axis	Variables	Coefficients (%)*
1	Air Temperature-1	34.9
	Burlese Volume	21.6
	Humidity-1	12.8
2	Big Trees-Number	27.1
	Humidity-1	18.5
	Depth: Measured	16.5

Table 2 (continued).

3	Rainfall-Today	41.5
	Saplings-Number	11.6
4	Herp Number	34.9
	Burlese Volume	11.6
5	Rainfall-Today	25.5
6	Buttress Cover	29.9
	Log Cover	29.9
7	Log Diameter	17.8
	Lianes-Number	14.7
	Buttress Diameter	11.8
	Burlese Volume	10.9
8	Herp spp.	18.8
	Palms-Number	11.9
	Slope	11.7
9	Herb Cover	48.1
10	Log Diameter	16.5
	Buttress Diameter	15.5
	Herp spp.	12.2
	Lianes-Number	11.6
11	Palms-Number	19.2
	Log Diameter	11.3
	Starting Time	10.3
12	Herp spp.	19.0
	Herp Numbeer	17.2
	Humidity-1	13.1

: includes only those variables with a coefficient>10%

The forest has a distinct understory, with very large trees, saplings, and mature lianes and palms. Although the cacao has been fallow for more than twenty years, it has less vegetational complexity than the forest.

Analyses of variance were used to test for differences between the variables among 13 months of the study. The following variables have a significant effect associated with month ($p<.001$): Air temperature, Burlese volume, Measured depth, Humidity, Number of individuals, and Number of species.

The results of multigroup discriminant function analysis (canonical variates) using the 13 months of the study as the groups are found in Table 2. The first 5 axes are significant at the .05 level. The first canonical axis is comprised of the air temperature, humidity, and Burlese volume. In an environmental discriminant space the temperature, humidity, and volume of the leaf litter are the most different over the course of the year. The second axis relates to humidity and the depth of the leaf litter. It is not until the third axis that rainfall becomes an important contributor to an axis. Any strong seasonality in the amphibians and reptiles may therefore be due to a response to humidity and air temperature variability, or to changes in the volume and depth of the leaf litter.

Many of the environmental variables show variability within the year. The depth and volume of the leaf litter, and to a lesser extent the humidity and the herbaceous cover of the forest floor, appear to be seasonal. There are marked differences between the forest and the cacao. There are more palms, logs, buttress trees, lianes and saplings in the undisturbed forest than the cacao. The cacao lacks a well defined forest understory, and is probably at one point in a successional series that approaches a mature forest in leaf litter and understory. The air temperature, on the average, is higher and the litter is deeper in the cacao than the forest. These and other environmental factors are more variable, and therefore less predictable, in the cacao than in the more mature and stable forest. This does not imply that it is a more stringent environment. In fact, there were more amphibians and reptiles found in the cacao than in the forest. The cacao may constitute a perturbed system that is an excellent environment for some species and less so for others.

Amphibian and Reptile Species

Forty-seven species of amphibians and reptiles were collected in the 90 litter plots (Tables 3 and 4). Of the 47 species, 43 were found in the forest and 31 were found in the cacao. Only one-fourth of all the species (12/47) was found exclusively in the forest. There were more individual animals in the cacao than in the forest, with a total of 1193 in the cacao and 774 in the forest. This is reflected in a higher Shannon diversity index in the forest than the cacao (Table 5). The perturbed system, the cacao forest, supported a higher number of amphibians and reptiles than the forest. The more prevalent species in the forest were even more abundant in the cacao, while many of the rarer species either could not or did not succeed in the more disturbed habitat. The evenness component, J' (Pielou, 1966) is higher in the forest, both during the day and at night, than it is in the cacao.

The most abundant species in both environments were *Eleutherodactylus bransfordii* and *Dendrobates pumilio.* These two frogs are diurnal (Savage, 1981), yet were also captured in large numbers at night. Day-night differences should in fact be approached with reservation, since diurnal animals were still present in the litter at night and were collected along with nocturnal animals. The third and fourth most abundant species, both lizards, were *Norops humilis* and *Lepidoblepharis xanthostigma.* The frog *Gastrophryne pictiventris* is the next most abundant, with a total of 84 individuals in the 90 litter plots. It was rarely collected during the day (9 daytime versus 75 nightime occurrences), probably because it is fossorial and buries beneath the litter during the say (Savage, pers. comm.).

In all, there were 13 species with 12 or more individuals taken during the study. The remaining 34 species were represented by six fewer individuals each. The very high species richness is typical of the New World tropics, with a few very abundant species and many rare ones (Scott, 1976; Toft, 1980a; 1980b). In the Old World tropics the pattern is somewhat different. Inger (1980a; 1980b) did not find population densities as high as those recorded here, nor did he see a comparable numerical dominance of a few very abundant species. Perhaps the patchiness in the Old World localities is greater; the presence or absence of seasonality may impinge on this disparity.

There were up to 34 individual *Eleutherodacty-*

Table 3

SPECIES LIST
Taxonomic Breakdown

- Amphibia
  - Caudata
    - Plethodontidae
      - *Oedipina sp.*

  - Anura
    - Microhylidae
      - *Gastrophryne pictiventris* (Cope)
    - Leptodactylidae
      - *Eleutherodactylus:* Biporcatus group
        - *E. biporcatus* (W. Peters)
      - Cruentus group
        - *E. altae* Dunn
        - *E. caryophyllaceus* (Barbour)
        - *E. cerasinus* (Cope)
        - *E. cruentus* (W. Peters)
        - *E. ridens* (Cope)
      - Diastema group
        - *E. diastema* (Cope)
      - Fitzingeri group
        - *E. crassidigitus* Taylor
        - *E. fitzingeri* (O. Schmidt)
        - *E. talamancae* Dunn
      - Gollmeri group
        - *E. bransfordii* (Cope)
        - *E. gollmeri* (W. Peters)
        - *E. mimus* Taylor
        - *E. noblei* Barbour and Dunn
      - *E. sp.*
      - *Leptodactylus pentadactylus* (Laurenti)
    - Bufonidae
      - *Bufo haematiticus* Cope
    - Hylidae
      - *Hyla:* Albomarginata group
        - *Hyla rufitela* Fouquette
      - *Hyla:* Rubra group
        - *Hyla elaeochroa* Cope

Table 3 (continued).

- Dendrobatidae
    - *Dendrobates pumilio* Schmidt
    - *Phyllobates lugubris* (O. Schmidt)
- Centrolenidae
    - *Centrolenella:* Prosoblepon group
        - *Centrolenella prosoblepon* (Buettger)

Reptilia

- Squamata - Sauria
    - Gekkonidae
        - *Lepidoblepharis xanthostigma* (Noble)
    - Iguanidae
        - *Corytophanes cristatus* (Merren)
        - *Norops capito* (W. Peters)
        - *Norops carpenteri* (A.A. Echelle, A.F. Echelle & Fitch)
        - *Norops humilis* (W. Peters)
        - *Norops limifrons* (Cope)
    - Teiidae
        - *Ameiva festiva (*Lichtensteis & von Martens)
    - Xantusiidae
        - *Lepidophyma flavimaculatum* A. Dument
    - Scincidae
        - *Leiolopisma cherrei* (Cope)

- Squamata - Serpentes
    - Colubridae
        - *Amastridium veliferum* Cope
        - *Coniophanes fissidens* (Gunther)
        - *Dendrophidion vinitor* H.M. Smith
        - *Imantodes cenchoa* (Linne)
        - *Leptodeira septentrionalis* (Kennicott)
        - *Mastigodryas melanolumus* (Cope)
        - *Ninia maculata* (W. Peters)
        - *Nothopsis rugosus* Cope
        - *Pliocercus euryzonus* Cope
        - *Rhadinaea decorata* (Gunther)
        - *Sibon nebulata* (Linne)
        - *Trimetopon pliolepus* (Cope)
    - Viperidae
        - *Bothrops nasutus* Bocourt

Table 4

TOTAL NUMBERS OF INDIVIDUALS

		Forest		Cacao	
Species	**Total**	**D**	**N**	**D**	**N**
Eleutherodactylus bransfordii	693	134	130	237	192
Eleutherodactylus cerasinus	3	1	1	1	0
Dendrobates pumilio	476	62	77	192	145
Norops humilis	253	49	55	78	71
Lepidoblepharis xanthostigma	148	17	15	68	48
Gastrophryne pictiventris	84	8	55	1	20
Norops limifrons	57	16	11	14	16
Eleutherodactylus biporcatus	49	7	11	18	13
Leiolopisma cherrei	39	8	9	13	9
Eleutherodactylus talamancae	25	8	16	0	1
Eleutherodactylus diastema	21	5	6	7	3
Eleutherodactylus mimus	15	3	10	0	2
Eleutherodactylus ridens	15	2	2	8	3
Bufo haematiticus	12	2	6	3	1
Eleutherodactylus caryophyllaceus	6	5	1	0	0
Nothopsis rugosus	6	1	0	4	1
Ameiva festiva	4	1	1	2	0
Rhadinaea decorata	4	0	1	2	1
Norops capito	4	2	0	1	1
Oedipina sp.	3	1	1	1	0
Lepidophyma flavimaculatum	3	1	1	1	0
Ninia maculata	3	0	0	3	0
Eleutherodactylus sp.	3	3	0	0	0
Eleutherodactylus cerasinus	3	1	1	1	0
Eleutherodactylus cruentus	3	1	1	1	0

Table 4 (continued).

TOTAL NUMBERS OF INDIVIDUALS

		Forest		Cacao	
Species	**Total**	**D**	**N**	**D**	**N**
Hyla elaeochroa	3	1	1	1	0
Corytophanes cristatus	3	1	2	0	0
Eleutherodactylus gollmeri	3	0	3	0	0
Eleutherodactylus altae	2	0	2	0	0
Norops carpenteri	2	0	0	1	1
Leptodactylus pentadactylus	2	0	2	0	0
Eleutherodactylus crassidigitus	2	0	2	0	0
Eleutherodactylus fitzingeri	2	0	1	1	0
Coniophanes fissidens	2	0	0	1	1
Bothrops nasutus	2	0	1	1	0
Rhadinaea guentheri	2	0	0	0	0
Phyllobates lugubris	2	0	2	0	2
Dendrophidion vinitor	1	0	1	0	0
Mastigodryas melanolomus	1	1	0	0	0
Trimetophon pliolepus	1	0	0	0	1
Eleutherodactylus noblei	1	0	1	0	0
Leptodeira septentrionalis	1	0	0	0	1
Centrolenella prosoblepon	1	1	0	0	0
Amastridium veliferum	1	0	0	1	0
Sibon nebulata	1	0	1	0	0
Pliocercus euryozonus	1	1	0	0	0
Hyla rufitela	1	1	0	0	0
Imantodes cenchoa	1	0	1	0	0
TOTALS	1967	344	430	660	533

D: Day N: Night

Table 5

SHANNON-WIENER DIVERSITY INDICES

Month	#Species	#Individuals	H′	J′	Gleason
December 1973	17	117	2.129	.75	3.36
January 1974	15	156	1.943	.72	2.77
February 1974	13	210	1.835	.72	2.24
March 1974	21	192	1.991	.65	3.80
April 1974	18	193	2.026	.70	3.23
May 1974	17	256	1.692	.60	2.89
June 1974	16	153	2.004	.72	2.98
July 1974	17	137	1.890	.67	3.25
August 1974	18	109	2.138	.74	3.62
September 1974	14	82	1.814	.69	2.95
October 1974	13	83	1.748	.68	2.72
November 1974	14	87	1.973	.75	2.91
December 1974	17	192	1.763	.62	3.04

Group	#Species	#Individuals	H′	J′	Gleason
Forest-Day	28	344	2.099	.63	4.62
Forest-Night	33	430	2.292	.66	5.28
Cacao-Day	25	660	1.796	.56	3.70
Cacao-Night	21	533	1.801	.59	3.19

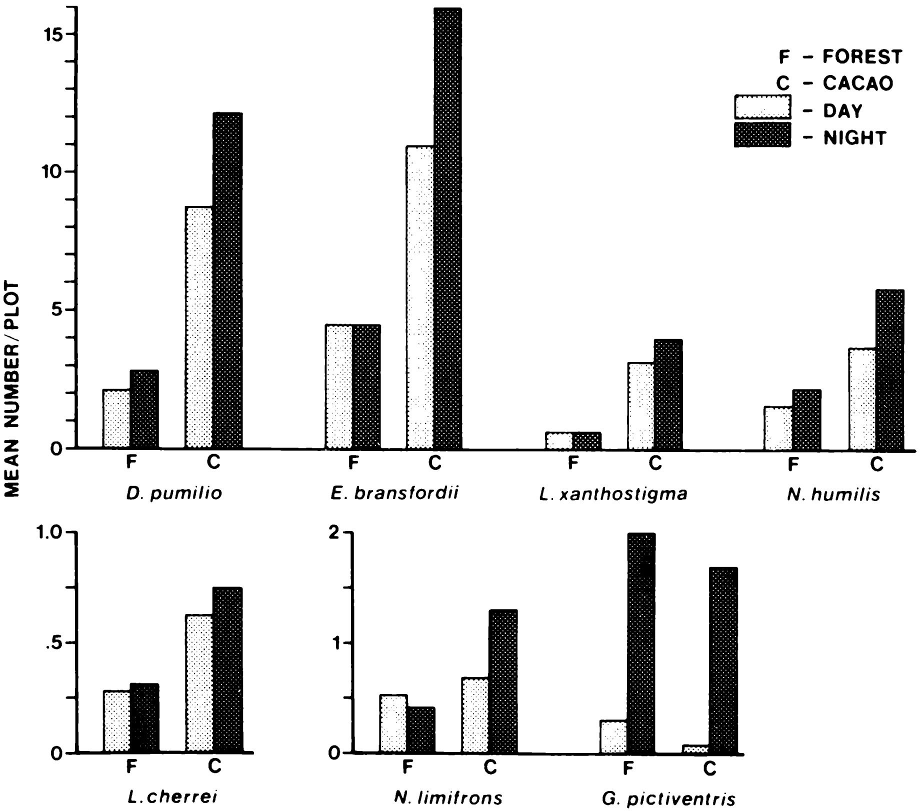

Figure 4

Mean numbers per plot of the seven most abundant species, separated into forest, cacao, day and night plots.

lus bransfordii in a single 8 x 8 meter plot. Figure 4 depicts the mean number per plot of the seven most abundant species, for four subsets of the litter plots: forest-day, forest-night, cacao-day, and cacao-night. The maxima for *Eleutherodactylus bransfordii* and *Dendrobates pumilio* were in the cacao and not the forest. The mean numbers per plot for the abundant species were greater in the cacao than the forest. Even among the more prevalent species, four were found in the forest and not the cacao at all. For example, *Eleutherodactylus caryophyllaceus* had six individuals at six different litter plots in the forest, and none in the cacao.

Figure 5 shows the distribution of the number of individuals per plot for the three most abundant species: *Eleutherodactylus bransfordii, Dendrobates pumilio,* and *Norops humilis.* In the forest, *Eleutherodactylus bransfordii* had from 0 to 13 individuals per plot, with a majority of the plots having four or fewer individuals. In the cacao there were from 0 to a maximum of 34 individual *Eleutherodactylus bransfordii* per plot. In a random cacao plot, it would be much harder to predict the number of *Eleutherodactylus bransfordii* one would expect than it would be in the forest. Such was also the case for *Dendrobates pumilio.* In the forest, there from 0 to 6 *Dendrobates pumilio* individuals per plot, but there can be up to 20 in the cacao. A similar pattern is found for *Norops humilis* as well.

Figure 6 shows the relationships between the number of species and the number of individuals per plot. The regressions for both the cacao and forest sites are significant, yet the slope is much greater for the cacao. For a given number of species one can predict a greater number of individuals in the perturbed system, the cacao. Initial impressions of these data might be that the cacao is a less favorable habitat, since it supports fewer species; or that the cacao is a more favorable habitat, since it supports a greater density of amphibians and reptiles, and probably a greater overall secondary consumer biomass per unit area, as well as a much greater density of certain important, if not ecologically dominant, species. The contention that one habitat is more or less favorable than another appears to be invalid and untestable.

Figure 7 shows how both the number of species per plot and the number of individuals per plot vary with the month of the year. The number of individuals peaks in January, during the dry season, and decreases throughout the end of the dry season and the onset of the rainy season. The number of individuals per plot is at its lowest in August,

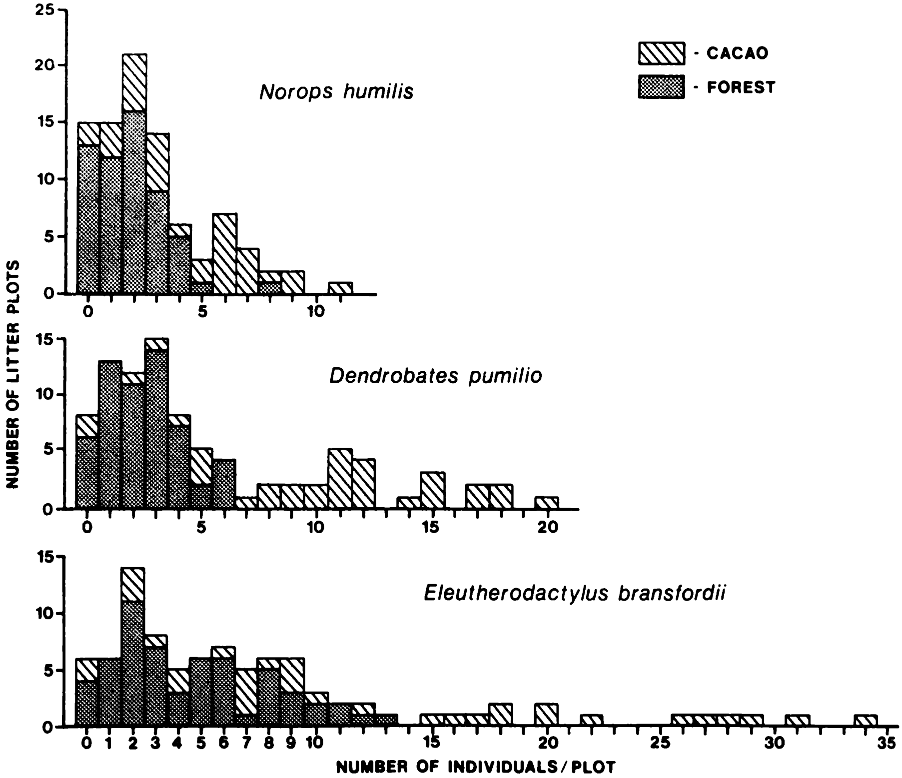

Figure 5

Abundances of the three most common species: Number of individuals per plot versus number of plots; forest and cacao separately.

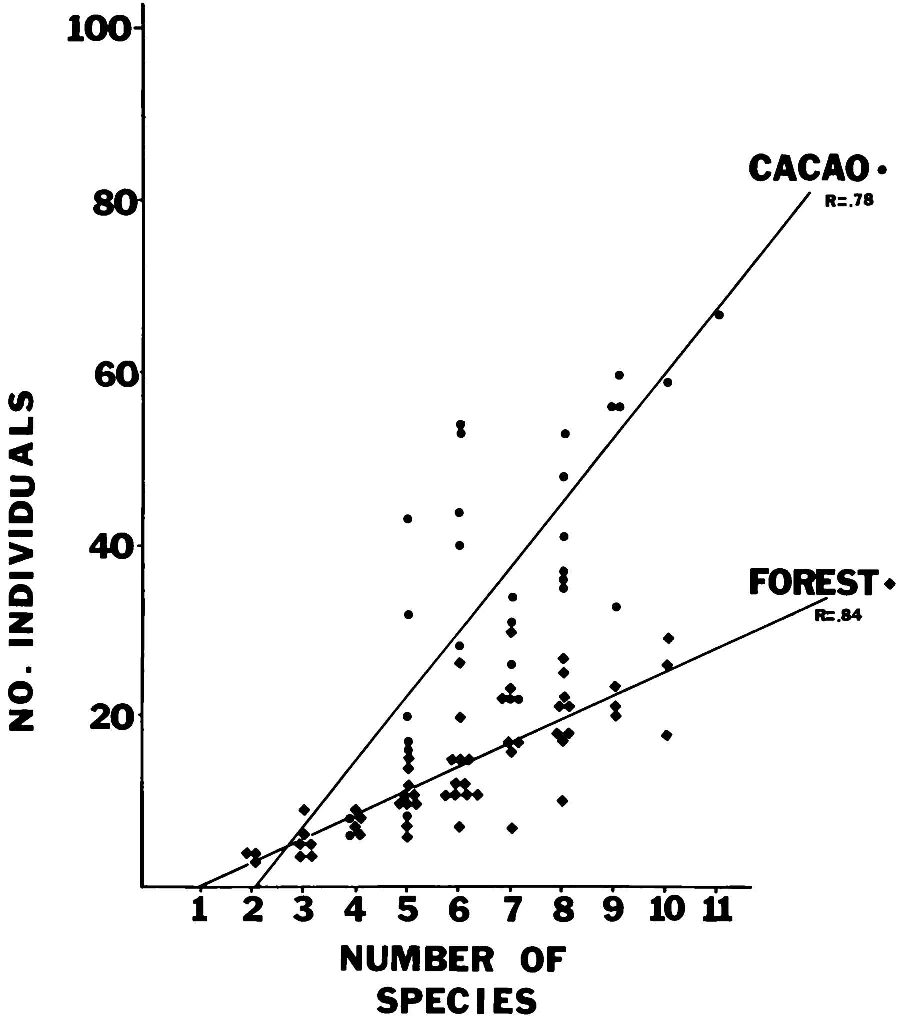

Figure 6

Relationship between the number of species and the number of individuals: forest and cacao. For both the forest and cacao regressions, R is significant at the .01 level.

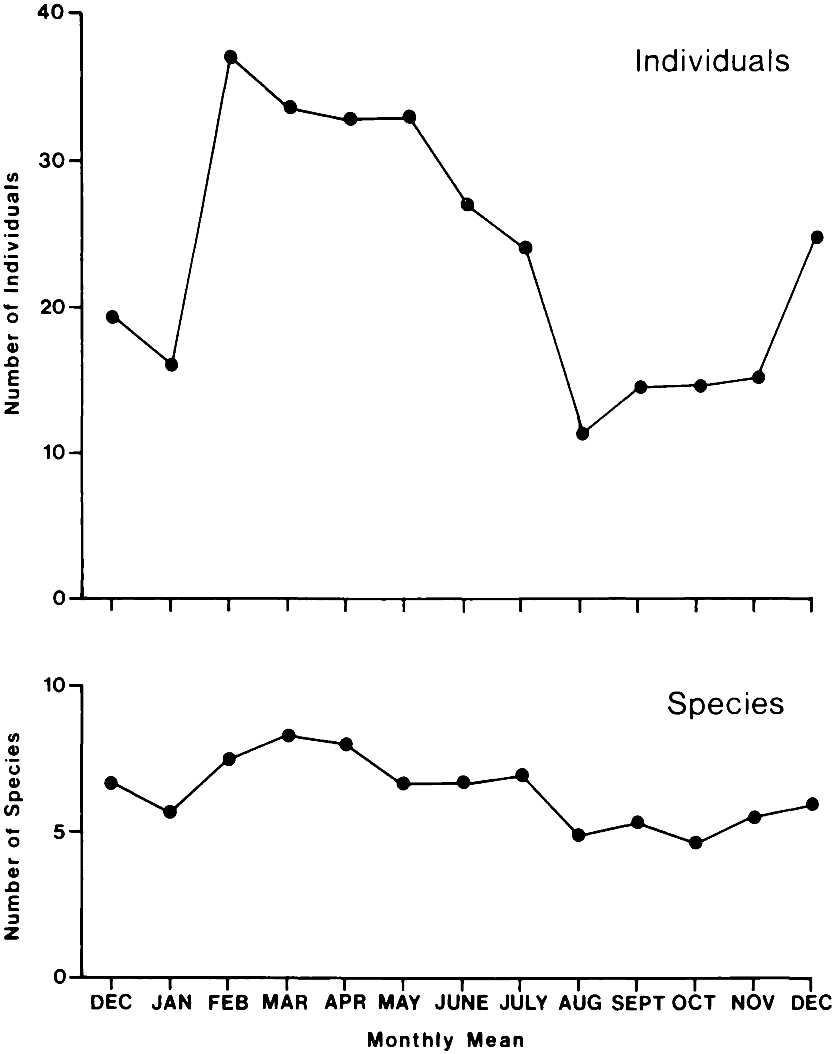

Figure 7

Monthly mean numbers of herpetofauna species and individuals, forest and cacao combined.

during the rainy season, and begins to increase in November, during the dry season. The number of species per plot peaks in March, at the end of the dry season, and decreases during the rainy season. An analysis of variance showed that the effect of month on the number of species is statistically significant. The seasonality of the number of individuals per plot is dramatically apparent in Figure 8, when the cacao and forest plots are separated. The large increase in number of individuals per plot occurs predominantly in the cacao, and much less in the forest. The seasonality apparent in Figure 7 has its main source from the cacao plots. The introduction of perturbation into the system, i.e. the cacao plantation, and its subsequent successional development, induces a greater seasonality than that found in the undisturbed ecosystem.

Figure 9 shows the monthly means for the five most abundant species. The densities of the most abundant species, in particular *Eleutherodactylus bransfordii,* were highest from February to May, at the end of the dry season, when the litter volume and herbaceous cover were highest. The pattern is consistent for all of the species. There were slight increases in abundance for *Eleutherodactylus bransfordii, Norops humilis, Dendrobates pumilio,* and *Lepidoblepharis xanthostigma* from November to December. This coincides with a dip in monthly and sampling period rainfall, and an increase in litter volume and humidity (Figure 3). Figure 10 shows the monthly total numbers of individuals for four of these species. This figure shows the peaks in abundance at the end of the dry season, in May.

The abundances of the major species of frogs and lizards in the leaf litter were seasonal, and correspond to the end of the dry season, the onset of the rainy season, and the volume fo the leaf litter. Perhaps the increased densities were a result of recruitment, or a response to increases in arthropod populations that result from the increased litter depth in the dry season. Such strong seasonality in both environmental factors and amphibian and reptile populations in a tropical wet forest dispels the notion that such forests are aseasonal. The seasonality is different from that in the temperate zone, but no less important. In a study of tropical succession, Ewel (1980) found that there are in fact more combinations of rainfall and temperature in the tropics than the temperate zone.

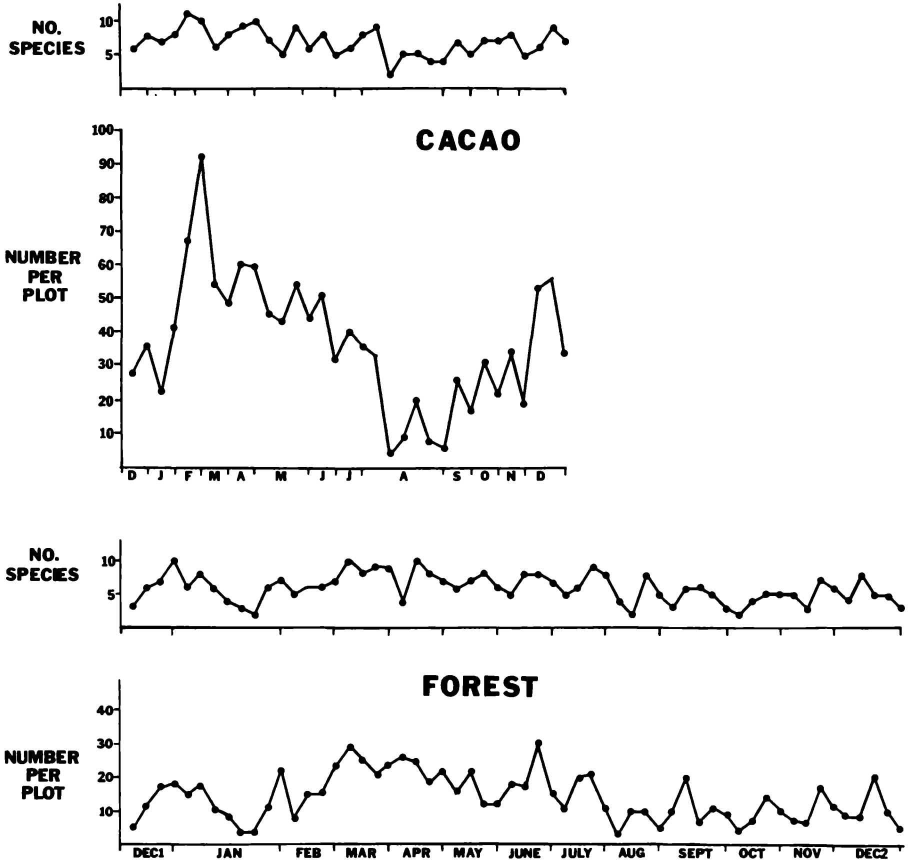

Figure 8

Monthly totals per plot of number of herpetofauna species and number of individuals. Forest and cacao plots graphed separately.

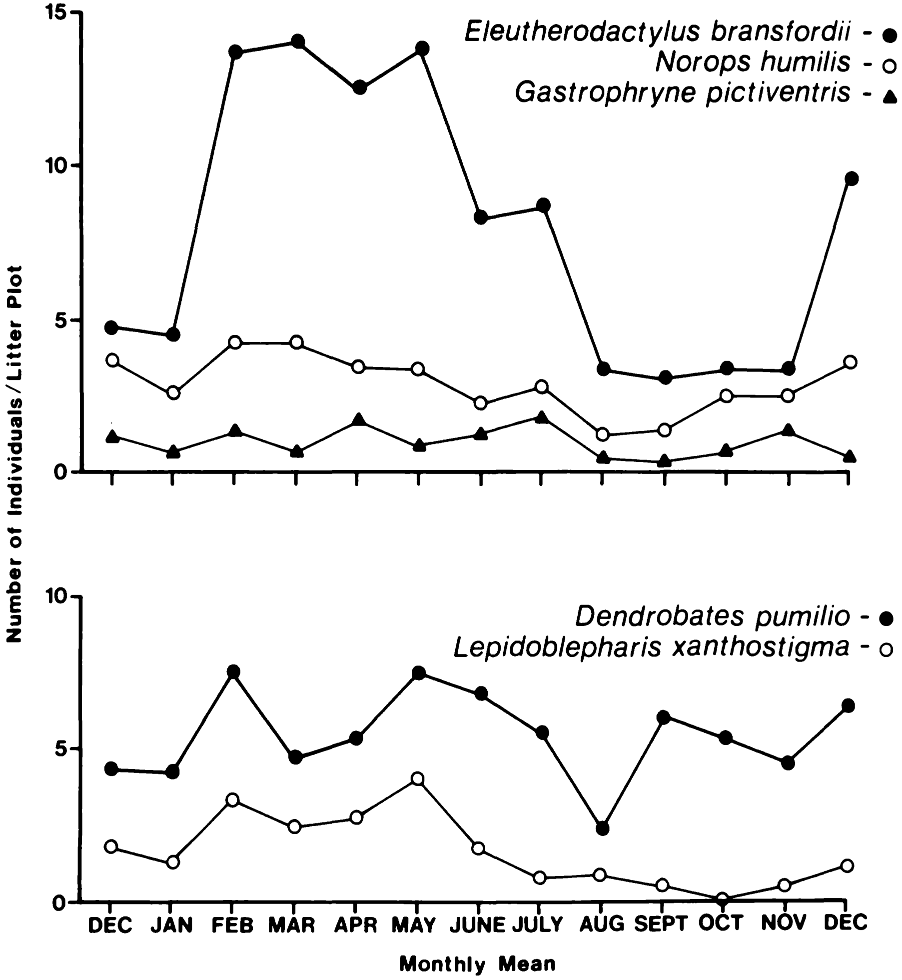

Figure 9

Monthly mean numbers of individuals per plot for the five most abundant species.

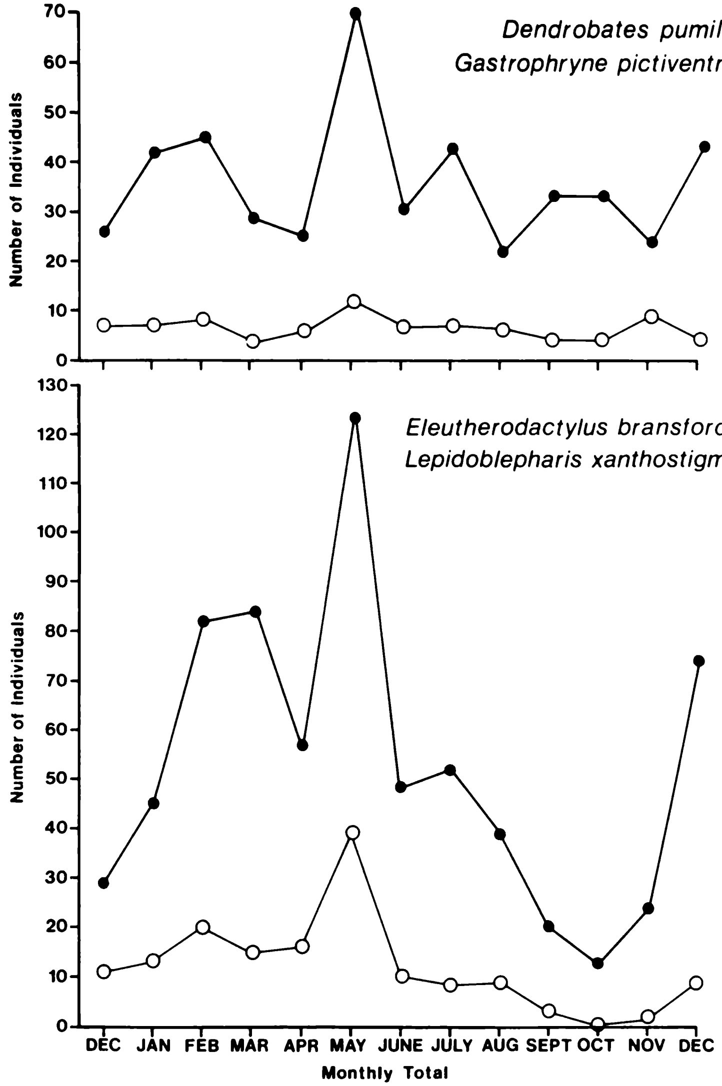

Figure 10

Monthly total numbers of individuals per plot for the four most abundant species.

Species and Environmental Variables

There are high correlations between the abundances of all the major species except *Bufo haematiticus* and *Leiolopisma cherrei*. There are also high negative correlations between the abundances of most of the species and the number of palms. When the litter was deeper the abundances of most of the species were significantly higher. The only major species with a significant correlation with the number of big trees or buttress trees were *Bufo haematicus* and *Lepidoblepharis xanthostigma*. Number of saplings correlates with the abundances of *Eleutherodactylus bransfordii* and *Lepidoblepharis xanthostigma* only. The only environmental variable that correlates with the abundance of *Dendrobates pumilio,* other than the number of palms, is the depth of the litter.

An analysis of variance tested for differences between the values of the environmental variables for any of the species. For all 90 litter plots, only four variables show a significant "effect" of species. They are: Starting time ($p=.009$), number of buttresses ($p=.03$), log cover ($p<.0001$), and rainfall ($p=.05$). For the cacao plots only, air temperature was also significant ($p=.05$), and for the forest plots only, big tree diameter was also significant ($p=.001$).

Normal and inverse cluster analyses were done on the species-site matrix of this study, using the techniques mentioned in the Materials and Methods section. Figure 11 is the dendrogram of species. Three major clusters are found. Figure 12 is the dendrogram of the cluster analysis of the sites. I have divided the sites into 7 groups, based on the clusters of the dendrogram. These groups will be used later for discriminant analysis. There are two main clusters, the first containing Group G only, the second all the rest. Group G has cacao sites only. A few cacao sites (6 of 33) are found in other clusters, but basically the distributions of the species are more similar in the cacao than elsewhere. The cacao sites are more similar to each other, based on amphibians and reptiles, than the individual months are to each other.

Table 6 gives the results of the canonical discriminant analysis on the environmental variables, using as groups the 7 site clusters from the dendrogram in Figure 12 (from the species-site matrix). This analysis was used to discern which environmental variables correspond to the pattern of sites that was found, and to show which of the

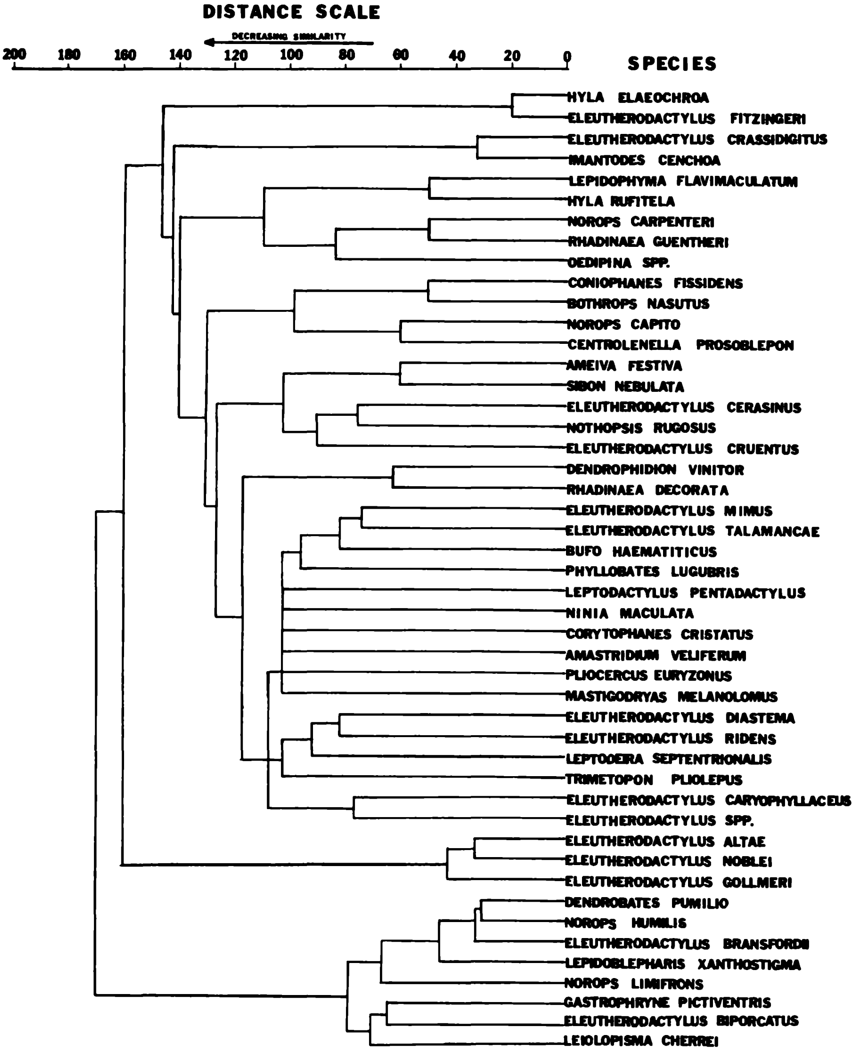

Figure 11

Classification: dendogram of species. Distance index used and clustering strategy are discussed in the text.

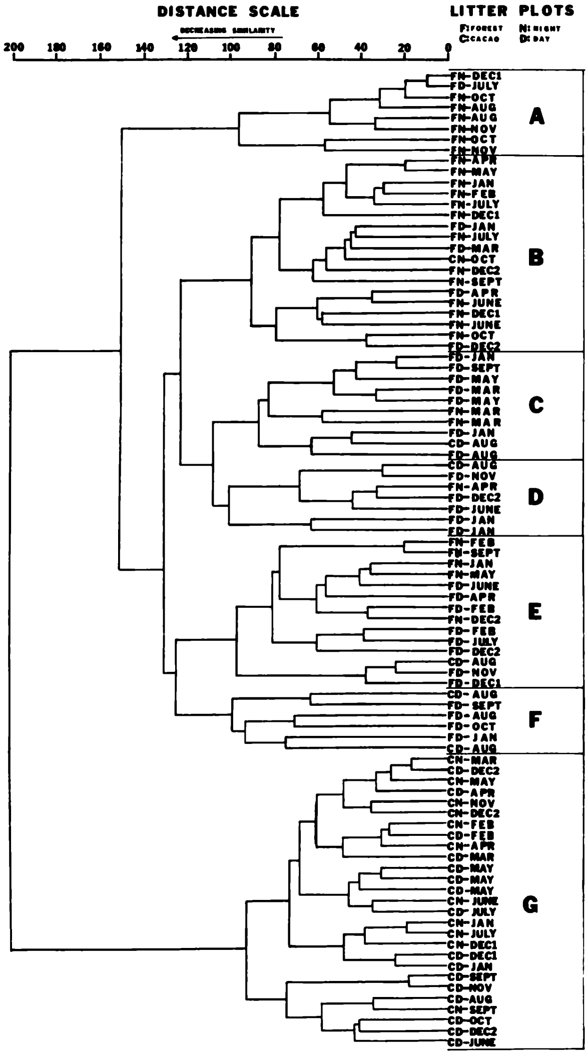

Figure 12

Classification: dendogram of sites. Distance index used and clustering strategy are discussed in the text.

environmental variables best describe the ampíhibian and reptile pattern (Smith, 1976; Green, 1971). The first 4 axes are significant at the .05 level. The first axis is determined by the number of amphibian and reptile species and the number of palms. Even when the herpnum variable is removed, this axis is still determined by the number of palms.

The scores on the first three axes for the 90 litter plots are graphed in Figure 13. Dendrogram Group G separates out on the first axis. This is the cluster of cacao sites. This indicates that the number of palms is the major factor that separates the forest and the cacao, and is most important to the amphibian and reptile species in the leaf litter. The number of palms should be of major consideration is any management approach to lowland tropical ecosystems. The second axis is determined by the time of day and the number of amphibian and reptile species. The second axis separates best Groups A, B, E, and G from Groups C, D, and F. Group A, which is very different on the dendrogram, separates out best on Axis 1. Group F, also somewhat disparate, separates out on Axis 2 only. Axis 3, in addititon to the number of species, is a rainfall axis, and differences in rainfall must account for much of the separation along Axis 3 in Figure 13. Differences in rainfall, as well as number of species, account for differences between dendogram Groups B, C and F, and the other 4. The fourth axis, not graphed, is determined by buttress cover, log diameter, and number of lianes. Litter volume or depth are not found in any of these axes, and cannot be said to be major factors contributing to any of the clusters in the dendrogram.

In summary, the null hypotheses that there are no differences in species abundances between the forest and the disturbed cacao, and between the months of the year, can be rejected with confidence. Significantly fewer species and more individuals were found in the disturbed cacao habitat. Significant correlations were found between several environmental variables and species abundances. The populations of the major species were determined to be seasonal. This study does not support the hypothesis that species rich habitats must have low evenness and little or no numerical dominance (Birch, 1981; MacArthur, 1969; MacArthur, 1970).

Table 6

MULTIGROUP DISCRIMINANT FUNCTION ANALYSIS
Latent Roots & Significance Test for Each Axis

Axis	Root	%	Cumulative %	Chi Squared
1	4.51	58.4	58.4	122.01*
2	1.32	17.1	75.4	60.08*
3	0.73	9.5	84.9	39.20*
4	0.51	6.6	91.5	29.45*
5	0.40	5.2	96.7	24.07
6	0.26	3.3	100.0	16.37

* designates a significant axis ($p < .05$)

VARIABLES CONSTITUTING AXES:
COEFFICIENTS OF SEPARATE DETERMINATION

Axis	Variables	Coefficients (%)*
1	Herp Number	57.1
	Palms-Number	13.3
2	Starting Time	24.9
	Herp spp.	20.5
3	Rainfall-total monthly	19.8
	Herp spp.	17.4
	Rainfall-3 days prior	10.7
4	Buttress Cover	16.4
	Log Diameter	*12.1*
	Lianes: Number	11.2
5	Buttress Number	17.9
	Big Tree Diameter	15.2
	Buttress Diameter	10.4
6	Rainfall-sampling period	20.3
	Rainfall-today	18.3
	Rainfall-total monthly	12.5

There are 7 groups, from hierarchical agglomerative classification of sites, based on species abundances.

*: includes only those variables with a coefficient>10%

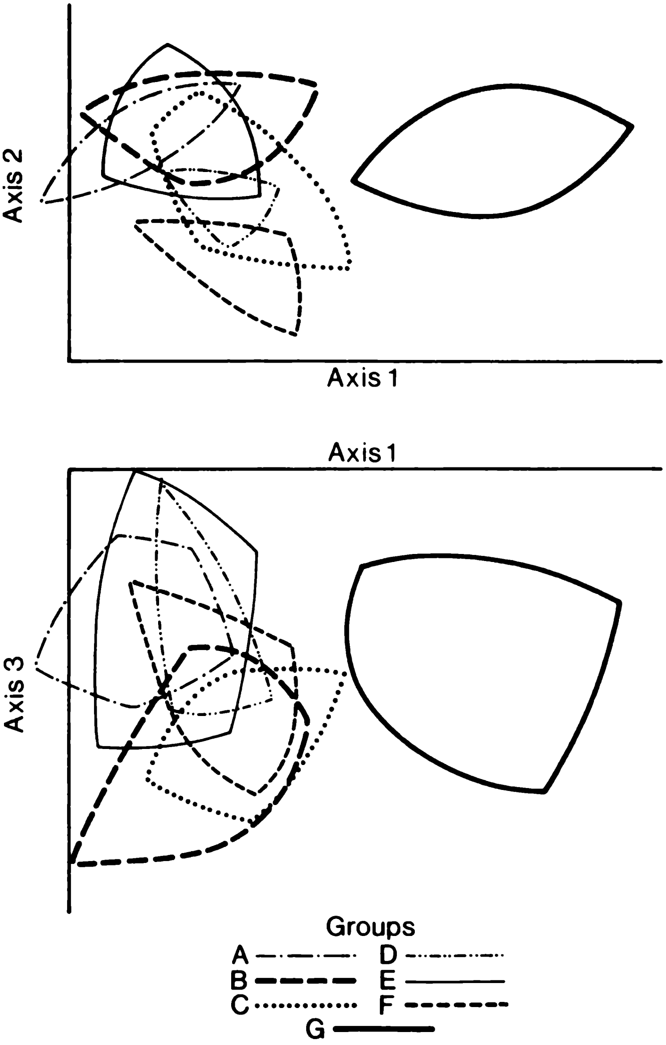

Figure 13

Discriminant analysis of seven site groups, using abiotic data. Groups are from the site dendrogram in Figure 12. Scores are given for the first three axes only.

Food Utilization: Stomach Contents

The stomach content results were evaluated first in terms of all frogs and lizards combined, and then by specific species. Table 7 lists the mean number per individual for each of the prey groups, but excludes zeroes from the calculations. For example, termites are a rare prey item; Yet, when they were eaten by *Gastrophryne pictiventris,* 14 of them were found in the stomach. *Bufo haematiticus,* for example, has an average of 21 mites per stomach, when mites are eaten. Such an approach allows a quick overview of the variability of prey taken by the frogs and lizards. It also allows one to see quickly that some species, such as *Dendrobates pumilio* and *Bufo haematiticus,* eat a large number of small prey. Others have fewer prey items per stomach, but a much greater variability of prey categories, such as *E. bransfordii,* with never more than 2, on the average, of any single prey category per stomach.

Table 8 lists the average prey lengths for individual frogs and lizards, again excluding zeroes from the calculations. Some species, such as *Dendrobates pumilio* and *E. ridens,* eat small ants, while others eat very large ants. *Leptodactylus pentadactylus* had an ant 11.5 mm long in its stomach! While no species had an average of more than 1.5 Hemiptera per stomach, the sizes of Hemiptera eaten varied from an average of 1.0 mm for *E. caryophyllaceus* to an average of 12.0 mm eaten by *E. mimus.* A similar wide range of size classes eaten is also found for the Orthoptera.

Some species, such as *Bufo haematiticus* and *Dendrobates pumilio,* had very little unidentifiable material. The majority of their diet is ants, which can be identified even from very small insect parts. The soft bodied arthropod prey are digested quickly, disintegrate and break apart in the stomach, and are often unidentifiable. From what could be identified, *Hyla elaeochroa* eats mostly Coleoptera, while 80.5% of the stomach contents were unidentifiable, and soft bodied prey may be under-counted. This must be kept in mind throughout the discussion. While soft bodied prey are probably underestimated in a consistent fashion, I have greater confidence in the absolute prey counts for the hard bodied ants, mites, Hemiptera, Homoptera, and Coleoptera. Because spiders are so distinct, I also have confidence in their counts.

Frogs and lizards are strict carnivores, and any plant material in their stomachs is unexpected, though it could be ingested

Table 7

MEAN NUMBER PER INDIVIDUAL: Part 1

(Zeroes not included)

FROGS	N	S-V	TOTAL	ANT	COLE	ORTH	SPDR	MITE	HYMN	DIPT	ISOP	HEMI	HOMO
Bufo haematiticus	11	31.1	24.7	21.4	1.3		2	21	1				
Centrolenella prosoblepon	1	22.0	2		1	1							
Dendrobates pumilio	26	20.1	34.8	23.1	1.2	1	1.7	13.8		1	1		
Eleutherodactylus altae	2	14.8	0										
Eleutherodactylus biporcatus	21	25.4	2.2	2	1.3	1	1		1		1.3		1
Eleutherodactylus bransfordii	52	17.8	2.5	1.7	1.1	1.2	1.2	1.4		1	1.7	1	1
Eleutherodactylus caryophyllaceus	5	18.3	1.7			1				1	1		
Eleutherodactylus cerasinus	3	17.3	2.5		1		2	1		1			
Eleutherodactylus crassidigitus	2	28.0	2			1				1	1		
Eleutherodactylus cruentus	1	16.5	3						1			1	
Eleutherodactylus diastema	17	12.9	3.4	3.2	1	1.5	2	1.7	1	1	1.3		
Eleutherodactylus fitzingeri	1	18.5	0										
Eleutherodactylus mimus	14	28.6	1.3			1					1	1	
Eleutherodactylus ridens	15	16.2	2.1	1.7	1		1.3	1	1		1		1
Eleutherodactylus talamancae	23	28.4	1.9	3		1.1	1.2			1	1		
Gastrophryne pictiventris	24	27.8	9.8	8.2	1.5	1	1	1	1	1		1	
Hyla elaeochroa	3	26.9	2.5		4								
Hyla rufitela	1	47.0	0										
Leptodactylus pentadactylus	2	35.0	2	1	1								
Phyllobates lugubris	2	21.5	7	7									
LIZARDS AND SALAMANDERS													
Ameiva festiva	3	62.7	1.3			1	1				1		
Corytophanes cristatus	1	94.0	0										
Leiolopisma cherrei	20	47.9	2.1			1	1.5		1	1	1.8	1.2	1
Lepidoblepharis xanthostigma	31	26.8	2.3			1.5	2	3		1	1	1	
Lepidophyma flavimaculatum	3	52.8	3	3									
Norops capito	4	63.8	1	1							1		
Norops carpenteri	2	29.0	0										
Norops humilis	26	27.1	1.9	1	1		1.4	1			1.7	1.3	1
Norops limifrons	23	34.3	2.1		1.7	2	1.3	2		1	1	1	1
Oedipina sp.	2	40.0	6	5	2								

N: number of stomachs sampled; S-V: snout-vent length; ANT: ants; COLE: Coleoptera; ORTH: Orthoptera; SPDR: spiders; MITE: mites; HYMN: Hymenoptera; DIPT: Diptera; ISOP: Isopoda; HEMI: Hemiptera; HOMO: Homoptera.

Table 7

MEAN NUMBER PER INDIVIDUAL: Part 2

(Zeroes not included)

FROGS	CENT	ARAC	DERM	APTE	WORM	VERT	TERM	L-D	L-C	L-L	L-?
Bufo haematiticus		1									1
Centrolenella prosoblepon											
Dendrobates pumilio											1
Eleutherodactylus altae											
Eleutherodactylus biporcatus			1			1		2	1		
Eleutherodactylus bransfordii	1	1	1					1	1		1
Eleutherodactylus caryophyllaceus										2	
Eleutherodactylus cerasinus											
Eleutherodactylus crassidigitus	1										
Eleutherodactylus cruentus											
Eleutherodactylus diastema		1									1
Eleutherodactylus fitzingeri											
Eleutherodactylus mimus	1						1			1	1
Eleutherodactylus ridens		1							1		
Eleutherodactylus talamancae		1				1			1		
Gastrophryne pictiventris	1	1			1		14				
Hyla elaeochroa									1		
Hyla rufitela											
Leptodactylus pentadactylus											
Phyllobates lugubris											
LIZARDS AND SALAMANDERS											
Ameiva festiva						1					
Corytophanes cristatus											
Leiolopisma cherrei	1	1							1		
Lepidoblepharis xanthostigma				1				2	1	1	
Lepidophyma flavimaculatum	2	1									
Norops capito											
Norops carpenteri											
Norops humilis	1	1							1		
Norops limifrons								1		1	
Oedipina sp.											

CENT: Centipedes and Millipedes; ARAC: Arachnids other than spiders and mites; DERM: Dermaptera; APTE: Apterygota; WORM: Worms; VERT: Vertebrates; TERM: Termites; L-D: Diptera larvae; L-C: Coleoptera larvae; L-L: Lepidoptera larvae; L-?: Unidentifiable larvae.

Table 8

AVERAGE PREY LENGTH: Part 1

(Zeroes not included)

FROGS	**N**	**TUML**	**ANT**	**COLE**	**ORTH**	**SPDR**	**MITE**	**HYMN**	**DIPT**	**ISOP**	**HEMI**	**HOMO**
Bufo haematiticus	11	13.0	3.7	4.8		3.0	0.4	4.0				
Centrolenella prosoblepon	1			4.5	2.5							
Dendrobates pumilio	26	6.1	1.4	1.7	2.0	0.8	0.7		1.6	2.0		
Eleutherodactylus altae	2											
Eleutherodactylus biporcatus	21	9.0	2.2	2.8	10.0	16.9		3.0		8.0		5.0
Eleutherodactylus bransfordii	52	5.8	2.5	2.8	5.9	2.7	0.6		2.6	5.4	1.5	3.3
Eleutherodactylus caryophyllaceus	5	8.0			17.0				1.0	1.0		
Eleutherodactylus cerasinus	3	7.2		3.8		4.8	0.5		2.0			
Eleutherodactylus crassidigitus	2	12.6			7.0				2.5	3.0		
Eleutherodactylus cruentus	1	7.2						1.8			6.0	
Eleutherodactylus diastema	17	3.9	1.1	2.0	3.0	1.0	0.9	1.0	1.0	2.1		
Eleutherodactylus fitzingeri	1	4.5										
Eleutherodactylus mimus	14	8.8			14.0					5.0	12.0	
Eleutherodactylus ridens	15	5.0	0.8	1.5		2.0	0.8	2.0		5.5		5.0
Eleutherodactylus talamancae	23	9.2	1.6		4.7	2.5			3.0	5.0		
Gastrophryne pictiventris	24	8.7	4.3	3.7	3.0	2.0	1.0	6.0	1.0		5.0	
Hyla elaeochroa	3	9.9		5.7								
Hyla rufitela	1	18.5										
Leptodactylus pentadactylus	2	10.0	11.5	3.0								
Phyllobates lugubris	2	7.3	3.1									
LIZARDS AND SALAMANDERS												
Ameiva festiva	3	14.3			18.0	4.0				3.0		
Corytophanes cristatus	1	30.0										
Leiolopisma cherrei	20	20.0			7.0	2.4		3.0	1.3	6.1	9.8	16.5
Lepidoblepharis xanthostigma	31	7.5			5.5	1.6	0.8		2.0	4.6	5.0	
Lepidophyma flavimaculatum	3	11.0	2.0									
Norops capito	4	14.3	4.5							5.0		
Norops carpenteri	2	6.8										
Norops humilis	26	7.9	2.9	3.3		2.4	0.7			4.4	6.5	4.5
Norops limifrons	23	8.2		3.1	3.4	2.4	0.5		2.1	3.6	6.5	2.0
Oedipina sp.	2	14.3	1.1	1.3								

N: number of stomachs sampled; TUML: Stomach length; ANT: ants; COLE: Coleoptera; ORTH: Orthoptera; SPDR: spiders; MITE: mites; HYMN: Hymenoptera; DIPT: Diptera; ISOP: Isopoda; HEMI: Hemiptera; HOMO: Homoptera.

Table 8

AVERAGE PREY LENGTH: Part 2

(Zeroes not included)

FROGS	**CENT**	**ARAC**	**DERM**	**APTE**	**WORM**	**VERT**	**TERM**	**L-D**	**L-C**	**L-L**	**L-?**
Bufo haematiticus		3.8									
Centrolenella prosoblepon											
Dendrobates pumilio										1.6	
Eleutherodactylus altae											
Eleutherodactylus biporcatus			16.0			34.0		4.0	3.5		
Eleutherodactylus bransfordii	13.3	2.5	7.0					2.0	3.5		2.7
Eleutherodactylus caryophyllaceus										8.0	
Eleutherodactylus cerasinus											
Eleutherodactylus crassidigitus	40.0										
Eleutherodactylus cruentus											1.4
Eleutherodactylus diastema		1.0						1.0	2.0		
Eleutherodactylus fitzingeri											
Eleutherodactylus mimus	11.0						3.6			5.0	10.0
Eleutherodactylus ridens		3.0							1.5		
Eleutherodactylus talamancae		6.0				14.0			13.5		
Gastrophryne pictiventris	9.7	4.0			18.0		10.0				
Hyla elaeochroa											
Hyla rufitela											
Leptodactylus pentadactylus											
Phyllobates lugubris											
LIZARDS AND SALAMANDERS											
Ameiva festiva						12.0					
Corytophanes cristatus											
Leiolopisma cherrei	10.5	2.0							4.5		
Lepidoblepharis xanthostigma				5.0				4.0	3.5	5.0	
Lepidophyma flavimaculatum	12.5	11.0									
Norops capito											
Norops carpenteri											
Norops humilis	9.0	3.3							1.7		
Norops limifrons								8.6		5.0	
Oedipina sp.											

CENT: Centipedes and Millipedes; ARAC: Arachnids other than spiders and mites; DERM: Dermaptera; APTE: Apterygota; WORM: Worms; VERT: Vertebrates; TERM: Termites; L-D: Diptera larvae; L-C: Coleoptera larvae; L-L: Lepidoptera larvae; L-?: Unidentifiable larvae.

accidentally during foraging, by being attached to an insect. A frog foraging in deep leaf litter might swallow some small leaf parts while capturing a prey item. No lizard had any plant material in its stomach, but 9 of the 20 amphibian species did. Fifty-five percent of the *Bufo haematiticus* and 33% of the *Gastrophyrene pictiventris* had plant material. This may reflect their methods of foraging. Both eat relatively large ants, several species of which cut and carry pieces of leaves that would be ingested along with the ant. This result implies that these species are active rather than passive foragers. In addition, of the 341 stomachs investigated, 7.3% were empty.

Table 9 lists the Shannon diversity indices (Shannon, 1964) for the numbers of prey. Those species with very high prey diversities are *E. bransfordii, Norops limifrons,* and *Norops humilis.* For the cacao alone prey diversity increases for some species, such as *E. biporcatus,* but decreases markedly for others, particularly *N. humilis* and *N. limifrons.* For all plots combined, the lowest prey diversities are found for *Hyla elaeochroa* and *Bufo haematiticus.* The two dominant species, *E. bransfordii* and *D. pumilio,* both significantly more abundant in the cacao than in the forest, have greater prey diversities in the cacao than in the forest. Mean prey diversity is also greater in the cacao than in the forest.

Table 10 lists the proportions of the different prey groups found in the stomachs of the 13 most abundant amphibian and reptile species, as well as the proportions of these arthropod groups in the leaf litter (Lieberman, 1982). The leaf litter arthropod data are from a concurrent study, at the same litter plots, both in the cacao and in the forest, which utilized can traps to evaluate arthropod populations. Arthropods were classified to the same level as the stomach contents discussed here (Lieberman, 1982). Table 10 does not include the stomach content data on those species with less than 12 individuals in the entire study. It is interesting to see what some rare species have in their stomachs, but the information cannot be used in any statistical comparisons. Table 11 shows the proportions of the different arthropods eaten and available in the leaf litter, for the 5 most abundant species, but for the forest and cacao separately.

Ants: In all the litter plots combined, *E. bransfordii* eats ants, the most abundant leaf litter arthropods, in roughly the same proportion as they are found in the habitat (31.5% compared with

Table 9

NUMBER OF PREY: DIVERSITY

Species	All Sites	Forest	Cacao
Eleutherodactylus bransfordii	2.195	2.084	2.125
Norops limifrons	2.022	1.841	1.424
Norops humilis	2.007	2.062	1.525
Eleutherodactylus biporcatus	1.975	1.519	2.151
Eleutherodactylus ridens	1.843	1.074	1.909
Eleutherodactylus mimus	1.834	1.677	0
Lepidoblepharis xanthostigma	1.815	1.535	1.755
Leiolopisma cherrei	1.765	1.318	1.605
Eleutherodactylus talamancae	1.692	1.671	0.693
Eleutherodactylus diastema	1.643	1.148	1.652
ALL SAMPLES	1.511	1.352	1.515
Ameiva festiva	1.386	1.386	–
Eleutherodactylus crassidigitus	1.386	1.386	–
Eleutherodactylus caryophyllaceous	1.332	1.332	–
Eleutherodactylus cerasinus	1.332	1.332	–
Lepidophyma flavimaculatum	1.011	0	0.673
Dendrobates pumilio	0.799	0.559	0.796
Gastrophryne pictiventris	0.694	0.793	0.461
Leptodactylus pentadactylus	0.693	0.693	–
Norops capito	0.693	–	0
Bufo haematiticus	0.502	0.114	0.983
Hyla elaeochroa	0.500	0.500	–
Oedipina sp.	–	–	0.637

Table 10

PROPORTIONS OF DIFFERENT ARTHOPODS PREY GROUPS IN THE DIETS OF 13 HERPETOFAUNA SPECIES AND IN THE LEAF LITTER

SPECIES

Prey Group	Dp	Ebr	Lx	Nh	Gp	Et	Nl	Ebi	Lc	Ed	Er	Em	Bh	LL
Ants	63.0	31.5		10.8	85.0	21.4		23.3		53.7	22.7		88.0	34.9
Coleoptera	0.9	11.7		2.7	3.9		18.5	30.2		1.9	9.1		1.9	4.4
Orthoptera	0.1	10.8	6.7		0.4	35.7	14.8	14.0	8.1	5.6		20.0		22.8
Spiders	1.2	11.7	40.0	27.0	0.4	21.4	29.6	4.7	16.2	11.1	36.4		0.7	5.1
Mites	34.0	6.3	13.3	5.4	0.9		7.4			9.3	9.1		7.9	0.6
Hymenoptera					0.4			2.3	2.7	1.9	4.5		0.4	0.6
Isopoda	0.1	9.0	17.8	27.0		3.6	3.7	9.3	40.5	7.4	4.5	10.0		1.2
Hemiptera		1.8	4.4	10.8	0.4		3.7		18.9			10.0		0.4
Homoptera		1.8					3.7	2.3	2.7		4.5			0.7
Centipedes		2.7		2.7	1.3				2.7			10.0		0.9
Arachnida		0.9		5.4	0.4	7.1			2.7	1.9	4.5		0.7	1.1
Dermaptera		0.9						2.3						0.4
Apterygota		2.2												18.1
Termites					6.0							30.0		0.2
Worms					0.4									0.3
Diptera	0.2	2.7	2.2		0.4	3.6	7.4		2.7	1.9				3.3
Larvae	0.4	8.1	13.3	8.1		3.6	11.1	9.3	2.7	5.6	4.5	20.0	0.4	3.7

KEY TO SPECIES

Dp : *Dendrobates pumilio*
E : *Eleutherodactylus*
Ebr : *E. bransfordii*
Lx : *Lepidoblepharis xanthostigma*
Nh : *Norops humilis*
Gp : *Gastrophryne pictiventris*
Et : *E. talamancae*
Nl : *Norops limifrons*
Ebi : *E. biporcatus*
Lc : *Leiolopisma cherrei*
Ed : *E. diastema*
Er : *E. ridens*
Em : *E. mimus*
Bh : *Bufo haematiticus*
LL : Leaf litter

Table 11

PROPORTIONS OF DIFFERENT ARTHOPODS GROUPS IN THE DIETS OF THE FIVE MOST ABUNDANT SPECIES AND IN THE LEAF LITTER: FOREST AND CACAO SEPARATELY

	D.pumi		**E.bran**		**L.xant**		**N.humi**		**G.pict**		**Leaf Lit**	
Prey Group	**F**	**C**	**F**	**C**	**F**	**C**	**F**	**C**	**F**	**C**	**F**	**C**
Ants	86.4	45.5	37.9	24.5			17.6	5.0	75.2	93.0	27.1	45.5
Coleoptera	0.6	1.1	10.3	13.2			5.9		7.6		3.6	5.4
Orthoptera	0.3		13.8	7.5	5.0	8.0					31.4	11.2
Spiders	2.6	0.2	10.3	13.2	45.0	36.0	23.5	30.0	1.0		5.8	4.1
Mites	9.5	52.4	3.4	9.4	25.0	4.0	11.8			1.6	0.7	2.1
Hymenoptera										0.8	0.5	0.8
Isopoda		0.2	6.9	11.3	10.0	24.0	5.9	45.0			1.3	1.2
Hemiptera			1.7	1.9		8.0	11.8	10.0		0.8	0.3	0.5
Homoptera			3.4								0.8	0.5
Centipedes			1.7	3.8				5.0	1.0	1.6	0.5	1.4
Arachnida				1.9			5.9	5.0	1.0		0.7	1.7
Dermaptera			1.7								0.2	0.7
Apterygota											19.7	16.0
Termites									13.3		0.2	0.2
Worms										0.8	0.3	0.4
Diptera	0.3	0.2	1.7	3.8	5.0				1.0		2.9	3.8
Larvae	0.3	0.4	6.8	9.4	5.0	20.0	17.6				3.5	3.8

F: FOREST C: CACAO

D. pumi : *Dendrobates pumilio*
E. bran : *Eleutherodactylus bransfordii*
L. xant : *Lepidoblepharis xanthostigma*
N. humi : *Norops humilis*
G. pict : *Gastrophryne pictiventris*
Leaf Lit : Leaf Litter

34.9%). Other species that eat ants in a similar proportion to that found in the leaf litter are: *E. biporcatus* (23.3%), *E. ridens* (22.7%), and *E. talamancae* (21.4%). Those species that eat ants in greater proportions than are found in the leaf litter are: *Bufo haematiticus* (88.0%), *Gastrophryne pictiventris* (85.0%), *Dendrobates pumilio* (63.0%), and *E. diastema* (53.7%). These same species also have ants as a high percent of total stomach biomass. Five of the six species of *Eleutherodactylus,* the most abundant genus, have over 20% of their diet comprised of ants. The differences between the species in numbers of ants eaten, percent of area, and length are significant at the .0001 level.

The above results are in contrast to what Toft reported for leaf litter frogs in Amazonian Peru (Toft, 1980b). She claimed that the dendrobatids and bufonids are ant specialists, because they eat mostly ants, yet found that they do not eat ants in an amount different from what is found in the leaf litter. I agree with Toft that dendrobatids and bufonids, as well as the microhylids, have a diet rich in hard-bodied ants and mites. Yet these prey items are taken in amounts significantly greater than found in the leaf litter. Toft looked at stomach contents only in the middle of the dry season and the middle of the rainy season, rather than throughout the year. My environmental results indicate that the end of the dry season, just prior to the onset of the rainy season, is the most critical period, in terms of change. Important information may be lost by not investigating the system at the end of the dry season, when arthropod food (litter volume, herbaceous vegetation, etc.) is most abundant and arthropod populations are maximal. Toft (1980a) stated that food is less abundant for the arthropods in the dry season, which conflicts with both my results and those of others working in New World lowland tropical sites (Bigger, 1976; Buskirk and Buskirk, 1976; Denlinger, 1980; Wolda, 1979).

In almost all cases, the ants eaten are much smaller than those found in the leaf litter. The possibility exists that small ants were under-sampled in the can traps (Lieberman, 1982), or perhaps other predators, possibly birds, may be eating the larger ants. It is also possible that many of the large ants in the leaf litter are army ants (Dorylinae), leaf cutter ants (Myrmicinae: Atta) which are very common, or large Pomerine ants, which may not have any predators. The ants eaten by *Dendrobates pumilio* (mean length = 1.4 mm) are much smaller than those eaten by either *Bufo haematiticus* (mean length = 3.7 mm) or *Gastrophryne pictiventris* (mean length = 4.3 mm). Those species of *Eleutherodacty-*

lus that eat ants in proportions similar to those in the habitat, eat ants of intermediate size, except for *E. ridens,* which also eats very small ants. This is a finer subdivision of the so-called "ant eating guild" (Toft, 1980a; 1980b). Those amphibians and reptiles that eat very many tiny prey items are probably spending a greater amount of their time actively foraging in the leaf litter than those that eat very few large prey items. It is difficult to call a species an ant specialist without any information as to the proportion of ant in the habitat, and the sizes of ants involved. The lizards eat few, if any, ants. Ants are most abundant at the end of the dry season, when the amphibians and reptiles are also most abundant. Whether the species that eat great numbers of ants do so because they prefer them, because they sit and wait for prey and ants are what happen to pass their way, or because they actively forage and ants are what they find, cannot be determined in this context.

Orthoptera: The second most abundant arthropods in the leaf litter are the Orthoptera, whose numbers also peak in April and May, just prior to the onset of the rainy season. Othoptera abundance is reduced in the disturbed cacao habitat (Lieberman, 1982). Only *E. talamancae* eats Orthoptera in a proportion greater than that found in the can trap samples (35.7% as compared to 22.8%) (Table 10). *E. mimus* is the only other species that eats Orthoptera in any proportion close to that in the habitat (20.0%). Several other species eat Orthoptera as well. The average percent of prey area and relative biomass of Orthoptera is great, even for those species that eat relatively few, such as *E. bransfordii* and *E. biporcatus.* The relative biomass of Orthoptera in the diet is significantly greater in those amphibians collected at night than during the day. The two species that rely heavily on orthoptera in their diets, *E. ridens* and *E. talamancae,* have significantly fewer individuals in the cacao than the forest. Orthoptera appear less able to succed in the perturbed habitat, and these two *Eleutherodactylus* may be affected.

Apterygota: Apterygota are the third most common arthropods in the leaf litter, comprising 18.1% of all individuals in the can traps (Lieberman, 1982), though their abundance is very unpredictable. They peak at the end of the dry season, accounting for a high overall percent of the leaf litter arthropod fauna. Apterygota decreased to zero in the beginning of the dry season. The only species eating any was

Lepidoblepharis xanthostigma, with one. Even though Collembola are hardbodied and easy to identify, and would be digested slowly by frogs and lizards. I am confident of the accuracy of these figures and that this group is not a prey item for amphibians and reptiles. They are probably very unpalatable, but may also be the preferred prey of some other leaf litter insectivore.

Spiders: Spiders are the fourth most common arthropod group in the can traps and the second most common (after ants) in the diets of the herpetofauna. Several species eat spiders in much higher proportion than found in the leaf litter (Table 10). These species can be considered to specialize on spiders. This is the first prey group discussed that the lizards eat in proportions higher than in the can traps. *Lepidoblepharis xanthostigma, E. ridens, Norops limofrons, Norops humilis, E. talamancae* and to a lesser extent *Leiolopisma cherrei* are spider specialists. Spiders are significantly more abundant in the forest than the cacao (Lieberman, 1982) and may be less adaptable to the greater seasonality and unpredictability of the disturbed system. The spider specialists substitute other prey in the cacao. *Norops humilis,* for example, eats a high proportion of spiders and is more abundant in the cacao. It eats mostly spiders and ants in the forest, but most of its diet in the cacao is Isopoda. Spider length, both in the leaf litter and the diet of the herpetofauna is extremely variable. The mean length in all the diets is 2.8 +/-6.1 mm. *E. bransfordii, E. biporcatus,* and *Norops limifrons* eat very large spiders. Among the spider specialists, *Lepidoblepharis xanthostigma* and *E. ridens* eat smaller spiders than the others. The arthropodivores in the leaf litter partition their food resources in that some species specialize or concentrate on spiders more than others; they even further partition the spiders. Those species that eat large numbers of spiders are probably active foragers, considering the rapidity with which spiders move within the leaf litter.

Miscellaneous Prey Groups: Several other prey groups are eaten in appreciable amounts by the amphibians and reptiles. Hemiptera are eaten significantly more by some species than others, particularly in the forest. Hemiptera are rare in the leaf litter (only 83 out of over 21,000 in the can traps), and are rarely, if ever, eaten by frogs. *Norops humilis* and *Leiolopisma cherrei,* eat large numbers of Hemiptera, however. *Lepidoblepharis xanthostigma* and *Norops limifrons* eat Hemiptera. None of these species had more than two individual Hemiptera per stomach. The same sort of pattern is found for the Isopoda, which are rarely eaten by frogs. Yet over 25% of the diets of *Norops humilis* and *Leiolopisma cherrei* was Isopoda. There was a maximum of six individual Isopoda per stomach.

In summary, the food source for the herpetofauna is partitioned. Some species eat prey in roughly the amounts found in the litter, some specialize or concentrate on small, hard-bodied ants and mites, some concentrate on large, solf-bodied prey such as Orthoptera, and others, all lizards, concentrate on hard-bodied, large prey such as Isopoda and Hemiptera. Other workers have shown such a wide spectrum of dietary preferences among sympatric anurans (Berry, 1965; Inger, 1961; Toft, 1980b; 1981).

There is no consistent relationship between snout-vent length or stomach length of the amphibians and reptiles, and the size or number of prey. *Dendrobates pumilio* and *E. bransfordii* are about the same size, but *Dendrobates* has an average of 35 small prey items per stomach, and *E. bransfordii* has an average of only 2.5 larger prey items per stomach. *Gastrophryne pictiventris* is about the same size as some of the larger *Eleutherodactylus* species *(talamancae, mimus, biporcatus),* but has more individuals per stomach, though not necessarily any smaller. There is a somewhat more predictable pattern among the lizards. They have only a few individuals per stomach, but the larger lizards (*Leiolopisma cherrei, Lepidophyma flavimaculatum, Norops capito)* eat larger prey. An exception is *Lepidoblepharis xanthostigma,* a small lizard that eats large prey. For those amphibians and reptiles that eat few prey items at a time, larger individuals eat larger prey and vice versa. For those that eat many prey items, and are probably foraging more actively in the litter, this is not the case.

Several authors have concentrated on amphibians alone (Toft, 1980a; 1981). The amphibians and reptiles completely co-occur within the leaf litter, and must be considered together. Both occupy the same kinds of forest floor microhabitat, though there is far more nocturnal activity in frogs. The increased sensitivity to low humidity and higher temperatures of frogs is another source of microhabitat variation between the two (Whittaker, 1973). Both feed on arthropods (Inger, 1980). I have shown that some amphibians have diets more similar to lizards than to other amphibians. Others have suggested, and I concur, that the inclusion in subsequent leaf litter analyses of some other important leaf litter arthopodivores, such as large spiders and some birds, would complete the picture (Scott, 1976). I do not claim that all of these species constitute a coherent, complete community. They are a large subset of those sympatric species utilizing the leaf litter habitat, and they partition the food that is available. When chi-square values were computed, all species considered ate the arthropods in proportions significantly different from those found in the can traps, at the .0001 level. The same is true of prey lengths. In a strict sense, none of the herpetofauna species are absolute dietary generalists. Each species has its own position along a continuum from absolute specialist to absolute generalist.

Ecology of Major Species

ELEUTHERODACTYLUS BRANSFORDII

Eleutherodactylus bransfordii is the most abundant leaf litter vertebrate in the rain forest at La Selva, comprising 693 of the 1967 individuals collected. It is a small frog found in humid lowland and subtropical forests from Honduras to Panama (Savage, 1970). It is diurnal, and actively hops across the leaf litter during the day, and dives under it when disturbed. It lays terrestrial eggs which, like all members of the genus *Eleutherodactylus,* undergo direct development and bypass the tadpole stage. It is also know to frequent streams more during the dry season (Savage, 1970; 1981). It was found at a density of 4.6 +/-3.4 in the undisturbed forest and 13.0+/-9.8 in the cacao. The distribution of these densities was much more normal in the forest. The density of this species is patchier and much less predictable in the disturbed ecosystem. It appears to be very successful at exploiting perturbed habitats. This could be because of any of the following, or a combination there of: the species has an inherently greater plasticity, the disturbed cacao habitat is more favorable physiologically, the arthropod prey in the cacao is preferable, predation is lower in the cacao, competition if any is reduced in the cacao, reproductive success is greater in the cacao, or recruitment is increased. Which of the above, if any, may be the case, cannot be ascertained at this time.

Direct development in *E. bransfordii* and its independence of temporary ponds could give it an ecological advantage in an unpredictable habitat (Heyer, 1973; Savage, 1970; Scott, 1976). It is most abundant from February to May, at the end of the dry season, when prey populations are highest, the litter is the deepest, and more herbaceous vegetation is present. Its increased abundance could be a response to increased prey populations. On the other band, *E. bransfordii* is cryptic, and avoids predators by diving beneath the leaf litter (Savage, 1980). This could predispose the frog to a preference for the deeper leaf litter of the cacao, and the deeper litter at the end of the dry season. Though all of the major frog and lizard species exhibited comparable seasonality, the trend is most dramatic for *E. bransfordii.* In any one month, no other species is more abundant than *E. bransfordii,* with the exception of *Dendrobates pumilio* from September thru November. When the environmental conditions favor greater numbers of *E. bransfordii,* they also favor increased numbers of the other major frog and lizard species.

E. bransfordii has a wide dietary range. It eats Coleoptera, spiders, mites and Isopoda in proportions significantly greater than those found in the leaf litter. It eats ants in the same proportion as they are found, and Orthoptera in a lower proportion than they are found in the leaf litter. Even though more ants are available in the cacao, *E. bransfordii* ate fewer ants in the cacao. More Coleoptera, mites, Centipedes, and arachnids were available in the cacao than in the forest, and more are eaten by *E. bransfordii.* A lower Orthoptera availability is followed by fewer Orthoptera being eaten as well. This supports the view that *E. bransfordii* is a dietary generalist. The sizes of prey taken by *E. bransfordii* are also variable, from small (0.6 mm) mites and spiders to large isopods and centipedes (up to 13.3 mm). As in almost all of the species, the mean prey length was less than that in the leaf litter. The mean prey length for *E. bransfordii* was 3.24 + /–2.51 in the forest and 3.26 + /–3.29 in the cacao. It consistently had few items per stomach (mean = 2.2 + /–1.6). It eats the highest prey diversity of any of the species, and this dietary diversity is greater in the cacao than in the forest. This is consistent with the concept that the less predictable, more variable habitat should allow or impel a species (that is capable of doing so) to become more of a food generalist.

Toft (1980a; 1981), from work in Panama, considered species of *Eleutherodactylus* to be in a “non-ant specialist” guild. I found instead that they eat ants in numbers not unlike those found in the leaf litter, and should be considered generalists. Toft’s (1980a) samples were from a few months only; she may have missed some of the seasonality of the diet. The seasonality and variability in the system promote a greater generalization by the species. My data dispute the hypothesis that dietary generalists should be "sit and wait" predators with low activity levels throughout the day (Toft, 1980a). *E. bransfordii* is a very active species, and most of this activity is probably foraging. The high proportion of ants eaten by *E. bransfordii,* equal to that of the leaf litter itself, indicates that it hardly avoids ants, but is able to prey on them. There is no mathematical or statistical basis for placing *E. bransfordii,* or any of the other species, into guilds. There is instead a continuum of species' prey utilization, from ant and mite specialists, to generalists, to species that specialize on other arthropod groups.

DENDROBATES PUMILIO

Dendrobates pumilio is the second most abundant vertebrate in the leaf litter, comprising 476 of the 1967 individuals. It is common in the Atlantic lowland forests of Central America (Savage, 1968). Its brightly colored legs contain skin alkaloids that are toxic and protect it from predators (Albuquerque, 1971). Like *E. bransfordii,* it is diurnal and terrestrial. Its eggs are laid in moist leaf litter (Savage, 1968), and the adults carry the tadpoles from the ground to water-filled bromeliads (Starrett, 1960; Young, 1979). It is more dependent on moist leaf litter than *E. bransfordii. D. pumilio* is known to maintain territories and have home bases (McVey, 1981). Like *E. bransfordii,* it is more abundant and dense in the cacao than in the forest, where its density is much less predictable. It also shows the same seasonal response. Both species are co-dominant, and cluster together in any classification dendogram. When conditions favor the increased abundance of one, they also favor the increased abundance of the other, though not necessarily for the same reasons. Unlike *E. bransfordii, D. pumilio* does not have to expend a lot of energy in prey avoidance, due to the toxins in its skin. I know no reason for it to prefer deeper leaf litter; the answer may lie in its differential prey utilizations.

D. pumilio eats predominantly ants, in proportions significantly greater than those found in the leaf litter. This is true of all the litter plots, but is particularly true for the forest. In the forest, 27.7% of the arthropods were ants, but a full 86% of all prey items of *D. pumilio* were ants. In the cacao, however, the proportion of ants is exactly the same as that in the leaf litter, which makes this species somewhat less of an ant specialist in the cacao. Instead, *D. pumilio* eats 52% mites in the cacao (versus 9% in the forest), to shift its prey dramatically in the disturbed habitat. There are more ants in the cacao, but these are large ants (Lieberman, 1982), and are probably not the ones that *Dendrobates* eats. The same occurs with two other frogs that prey on small ants, *E. diastema* and *Bufo haematiticus,* with a reduction in ant predation accompanied by increased mite predation, in the cacao. *D. pumilio* eats many small prey (mean number per stomach = 20.1). The mean prey length of *Dendrobates* is 0.77 +/–0.36 in the forest and 0.50 +/–0.35 in the cacao. The very small prey lengths in the cacao are biased by the mites. It actively forages in the litter (Savage, 1981; McVey, 1981), and appears to select the small ants and mites that it encounters. The large numbers of prey per stomach are consistent with a high level of activity. Certainly a preference for small, hard-to-digest prey such as ants and mites energetically necessitates very active rather than intermittent feeding behavior. This is supported by the fact that only one of the stomachs looked at was empty.

NOROPS HUMILIS

Norops humilis is the third most common member of the leaf litter herpetofauna, and the most common lizard, with 104 individuals captured in the litter plots in the forest and 149 in the cacao. It is a relatively common diurnal lizard in warm humid climates from the lowlands of Chiapas, Mexico thru Central America into eastern Panama (Fitch, 1973). *N. humilis* is primarily terrestrial, but is also common on low perches up to 60 cm from the ground (Talbot, 1979). All those collected in the litter plot could have spent some of their time above the leaf litter as well. For such a predominantly terrestrial species, the distinction isn't critical. Like *E. bransfordii* and *D. pumilio, N. humilis* is more abundant in the cacao, with higher yet patchier and more unpredictable densities. *N. humilis* has been found experimentally to prefer leaf litter over grass cover, and relatively low light intensities (Talbot, 1977). It is considered to be narrowly adapted to deep shaded habitats rich in leaf litter (Talbot, 1977). It is very successful in the disturbed cacao habitat, which has greater litter depths and volumes at certain times of the year. Talbot (1979) showed that *N. humilis* partitions habitat rather than food parameters, with respect to other congeners at least, and evinces no competitive interference. Though it is known to be very abundant around the buttresses of large trees (Fitch, 1973), I found it in plots with the average number of buttresses. *Norops carpenteri,* on the other hand, is a rare species that is found only when the number of buttresses in a plot is very high.

N. humilis has a varied diet. It east fewer ants than are available, and may be selectively avoiding ants and choosing other larger prey. This is particularly true in the cacao, where 45% of all arthropods are ants and *N. humilis* eats only 5% ants. The species preys heavily on spiders (27%) and Isopoda (27%). This is again more pronounced in the cacao, with 30% spiders and 45% Isopoda in the diet. *N. humilis* only has a few larger prey items in its stomach at any one time. The mean prey length is 2.9+/–1.9 mm in the forest and 4.0+/–2.6 in the cacao. The greater prey size in the cacao may be due to the proportionately higher predation on Isopoda. It is probably actively foraging and selecting specific prey items. It has a high prey diversity in the forest; its prey diversity is much lower in the cacao (as is that of *Norops limifrons*). Perhaps it does much better in the cacao than in the forest, because it can switch its prey and become more of a dietary specialist, with 75% of its diet in the cacao comprised of spiders and Isopoda only. In the forest *N. humilis* eats an average of 17.6% ants, 23.5% spiders, 5.9% Isopoda, 11.8% Hemiptera, and 17.6% larvae, representing a generalized diet (Table 10). It becomes a dietary specialist in the cacao, eating only 5% ants, no longer eating any Hemiptera, Coleoptera, mites, or larvae, but eating 30% spiders and 45% Isopoda. Though Talbot (1977, 1979) claimed that any partitioning between *N. humilis* and its congeners is related to optimal structural habitat choice and spatial factors, in a disturbed habitat, I claim that food and optimal diet choice are also important.

Like the other species, populations of *N. humilis* are seasonal, though ther effect is somewhat reduced. It increases in abundance from February to April, as do *D. pumilio* and *E. bransfordii,* when rainfall is lowest and litter depth and vegetation are highest. The actual mechanism for this seasonality is unclear. There is some evidence that lizards respond to reduced resources thru differential reproduction. Ballinger (1977), working on other iguanid lizards, found that in years of reduced food availability, the lizards had less fat storage prior to reproduction and resultant smaller and fewer clutches.

NOROPS LIMIFRONS

Norops limifrons, a diurnal lizard found in lowland deciduous and evegreen forests from Mexico to Panama, is most common in old second growth (Savage, 1981). It is mostly found 1-2 meters from the ground, but visits the leaf litter (Talbot, 1979). The 57 individuals collected in the 90 litter plots are transient visitors to the leaf litter (Talbot, 1977, 1979; Savage, pers. comm.). Whether those found in the leaf litter spent all or part of their day there, and their stomach contents represent leaf litter predation, or the were just "passing through" cannot be determined. Any comparison of their diet, or that of any of the other arboreal species found in the litter, with the can trap samples, must be minimal. Experiments indicate that *N. limifrons* has a broad ecological spectrum of tolerances and preferences (Talbot, 1977). It prefers high intensities and grass cover to the low light intensities and deep litter of the forest itself. It does well in disturbed habitats, such as cut or fallowed fields (Talbot, 1977). However, no forest/cacao differences were found in abundance.

The diet of *N. limifrons* is similar to that of *N. humilis,* with a high percentage of spiders. *N. limifrons* eats over twice as many spiders, proportionately, in the cacao than in the forest. Unlike *N. humilis,* it eats no ants, few Isopoda, and several Orthoptera, though it eats Orthoptera in the forest only. It eats Coleoptera in relatively high proportions. These dietary differences may represent differential availabilities of arthropods at the higher perch sities that *N. limifrons* prefers. It eats a high diversity of prey in the forest and a very low diversity in the cacao, just like *N. humilis.* In the forest *N. limifrons* eats mites, Orthoptera, Hemiptera and Homoptera, but eats none of these in the cacao; it eats 41.7% spiders in the cacao. It is the only species with any appreciable predation on flies, though this may again reflect arboreal rather than forest floor predation. If utilizations of the food dimensions of the niche are viewed as a continuum from specialist to generalist, *N. limifrons* and *N. humilis* shift position along this continuum, towards the specialist end, in a more disturbed habitat. This is contrary to a trend of fewer specialists in disturbed, less predictable habitats (Wiens, 1977).

LEPIDOBLEPHARIS XANTHOSTIGMA

Lepidoblepharis xanthostigma is the fourth most common member of the leaf litter herpetofauna, and is much more common in the cacao than the forest. It is a small, common diurnal terrestrial lizard often found near streams and frequently found is second growth. It is found in lowland evergreen forests from Costa Rica to Western Colombia (Savage, 1981). In those litter plots where it was found, the number of palms, saplings and logs were lower than average, and the litter was deeper and more voluminous. It does better in the higher habitat heterogeneity of the cacao, with its paucity of palms and saplings and increased litter depth. *L. xanthostigma,* like *N. humilis* and *N. limifrons,* specializes on spiders (40% of the diet); it eats a higher than expected proportion of Isopoda and mites. The increased mite predation is in the forest (25%) only, while Isopod predation in the cacao is more than twice that of the forest. It eats no ants or Coleoptera. All of its prey consists of soft-bodied arthropods, with the exception of Isopoda. Yet Isopoda in the stomach are well digested (personal experience), unlike the almost completely intact ants and Coleoptera found in those species that eat them.

GASTROPHRYNE PICTIVENTRIS

Gastrophryne pictiventris is a frog about which little was known and which was considered very rare prior to this study (Savage, pers. comm.). It is fossorial and nocturnal, and buries beneath the litter during the day (Charles Dock, pers. comm.). Only 9 of the 84 individuals found were captured during the day. It is also significantly rarer in the cacao, and would not be expected to be found in an even more disturbed habitat. I hypothesize that its numbers may increase in the cacao as that habitat undergoes successional processes. *G. pictiventris* is found in litter plots that have fewer large trees, and more palms, saplings, logs, lianes and herbaceous vegetation; it may be a habitat specialist. It is a dietary specialist, with 85% of its diet comprised of large ants. This is very obvious in the cacao, where a full 93% of its diet was ants. More ants are available in the leaf litter in the cacao as well, but of all the species specializing on ants, only *Gastrophyryne* had a concommitant increase in ant predation. Perhaps the ants in the cacao that were more abundant than in the forest were the very ants that this species eats. In all cases, *Gastrophryne* ate few relatively large ants (up to 9 mm). The mean prey size was 4.5+/–3.9 in the forest and 3.2+/–2.7 in the cacao. None of their stomachs was empty, and 33% contained some plant matter. The large Pomerine-like ants that these highly specialized frogs eat are currently being identified for further study (Roy Snelling, pers. comm.). Microhylids elsewhere have been found to eat termites as well (Inger, 1961). Only 6% of *Gastrophryne's* diet was termites (in the forest only), but this is high considering the relative paucity of termites in the leaf litter arthropod fauna.

SYNECOLOGICAL CONCLUSIONS

Amphibians and reptiles are much denser in the New World tropics than in the Old World tropics (Inger, 1980a; Scott, 1976; Heatwole, 1966). The frogs of Borneo are nocturnal (Inger, 1980a; 1980b), in contrast to the very high densities and species richness of diurnal frogs in the La Selva leaf litter. The terrestrial and diurnal niche occupied by *Eleutherodactylus* may be unexploited in the Indo-Malayan forests. Scott (1976) thought that the radiation of *Eleutherodactylus* in the New World is analogous to that of the skinks (Scincidae) in the Old World. However, the skink-dominated forests of the Old World do not approach the population densities of New World tropical forests.

Scott (1976) claimed that the higher densities in New World forests are inversely correlated with the number of species; I have shown the opposite is the case. Scott also noted that Old World tropical forest have more non-herpetofaunal competitors that limit populations. He suggested that analysis of ecologically and trophically similar species of ants, spiders, centipedes, onychophorans, birds, and mammals, are also necessary. He hypothesized that the leaf litter arthropod-eating consumer "aggregate" in the Old World tropics would have a comparable density to that in the neotropics. This hypothesis is worthy of further study.

In Borneo, Inger (1980a, 1980b) found frog densities two to three times greater in disturbed forests than in adjacent undisturbed forests. I propose that the neotropical forests that have been studied, such as those in Central America (Scott, 1976; Heatwole, 1966; Toft, 1980a), are more recent and/or more disturbed than their Old World or South American counterparts, and thus have a greater chance of species turnover.

Reduced litter production in Bornean forests has been proposed (Janzen, 1974; Bray, 1964) as a cause of the disparities in density between Old World and Central American rain forests (Inger, 1980b). However, the impoverished flora and litter production found by Jansen are atypical (Kira, 1967; Inger, 1980a; 1980b). Litter production values in the various tropical rain forests of the world are not significantly different (Kira, 1967). The Indo-Malayan rain forests have a higher proportion of trees of the family Dipterocarpaceae (Ashton, 1964; 1969), with a syncronized mast fruiting unknown in neotropical rain forests (Hartshorn, 1980; Inger, 1980a; 1980b). Janzen (1974) suggested that the "purpose" of the mast fruiting is to satiate seed predators. Inger suggested (1980a; 1980b) that the lower abundances in these forests are a result of mast fruiting, and not a cause. Inger contended that mast fruiting leads to reduced abundances of arthropods during non-mast years (Inger, 1980a). This situation will affect insect populations and in turn limit populations and densities of insectivores including frogs and lizards, and may in part explain the high densities of frogs and lizards found in the neotropics.

Though densities of individuals in Old and New World tropical forests are disparate, the number of species of frogs and lizards per unit area are approximately the same. The main difference is in the degree of dominance, which is intricately related to diversity in the conceptual framework of ecology (McNaughton, 1970). There is high species richness in the leaf litter (47 species of frogs, lizards, and snakes); however, of the 1967 individuals collected, 72.3% of them were representatives of only three species (35.2% *Eleutherodactylus bransifordii,* 24.2% *Dedrobates pumilio,* 12.9% *Norops humilis).* The remaining 44 species comprise only 27.7% of the individuals. There is therefore a high degree of dominance, both empirically and intuitively. This trend is more pronounced in the cacao than the forest.

Some authors claim that large numbers of species only occur with low abundance per species and resultant low dominance (MacArthur, 1955; 1969; Cody, 1968; 1975; Schoener, 1974), based on the assumption that very specialized species are not numerically dominant (May, 1973; 1974). Brich (1981) showed that in numerous marine systems, there is a tendency for greater dominance in species rich communities; my results support this view. *Dendrobates pumilio* is numerically abundant, and has an extremely specialized diet. Species-rich assemblages have been thought to preclude high species abundances based on theories of niche packing and competition. However, in the La Selva system there is no reason to assume competition and no way to show it without experimental evidence. In the absence of competition and/or limiting resources, there is no reason why systems with many species cannot have very high abundance and subsequent dominance of a few extremely successful species.

Fluctuating environments are claimed to support low diversity (Abrams, 1979), because of either low evenness and higher dominance, or low species richness, or both. Perhaps the rain forest at La Selva is more fluctuating and unpredictable than the Old World rain forests. The cacao forest is more unpredictable and has a lower evenness, lower species richness, and lower diversity than the undisturbed forest. High diversities are maintained in coral reef fish communities in the presence of non-equilibrium conditions (Talbot, 1978), for example, and perhaps these non-equilibrium conditions are predictable to the biota. Even though the forest is more predictable, it is not necessarily at equilibrium.

Sumary

The leaf litter herpetofauna, both in terms of its structural and physical environment and its diet, was studied over a period of 13 months at the lowland tropical research station at La Selva, Costa Rica, both in an undisturbed forest and an adjacent fallow cacao plantation. The cacao is considered disturbed based on the human perturbation by introduction of an agroecosystem. For many of the environmental variables, differences were found between the forest and cacao, between the day and night litter plots, and between the various months. Rainfall, litter depth and volume, humidity, and herbaceous cover are seasonal, for example. There are more palms, logs, buttress trees, lianes, and saplings in the forest than the cacao. The litter itself is deeper in the cacao than the forest, and the cacao lacks a well defined forest understory. In terms of environmental parameters, the cacao is concluded to be a more variable and less predictable habitat. This in no way implies that it is more stringent or inhospitable, however.

Forty-seven species of amphibians and reptiles (1967 individuals) were collected. Differences in numbers of species and individuals were found between the forest and cacao, the day and night plots, and the 13 months. There were more species in the forest, which had the highest diversity. The cacao had a higher overall abundance, density per plot, and degree of dominance. All of the five most abundant species had greater total numbers, patchiness, and density in the cacao than the forest. The degree of dominance found in the cacao and forest habitats is much higher than that known for Old World tropical leaf litter ecosystems. Total numbers of species and individuals, and total numbers of individuals of the main species, are strongly seasonal; they peak at the end of the dry season, when the arthropod populations are maximal and the leaf litter is deepest.

The arthropod food source for the herpetofauna is partitioned. In a comparison of stomach contents with can trap results, some species eat prey in roughly the same amounts as they are found in the leaf litter. Some eat mostly small, hard-bodied ants and mites, others eat mostly large, soft-bodied prey. Some of the ant specialists, such as *Dendrobates pumilio,* eat many very small ants; others, such as *Gastrophryne pictiventris,* eat very few large ants. The specific diets of the main herpetofauna species were discussed at length.

The two most abundant species, *E. bransfordii* and *D. pumilio,* had denser and patchier distributions in the cacao than the forest. The diets of these two dominant species are different: *E. bransfordii* eats very few large prey in proportions similar to those in the habitat, while *D. pumilio* eats only small ants and mites. I hypothesize that these two species are more successful in more perturbed, less predictable habitats. I hypothesize that early in the fallowing of the cacao plantation, there was even more dominance by these two species, and their forest and cacao populations will approach equality with time. I recommend further study to determine what limits the populations of these two species. It is possible to hypothesize that they are limited by competition with other species, but I very strongly doubt that this is the case. I hypothesize that the populations of *E. bransfordii* are limited by predator pressure. *D. pumilio,* which has toxic skin alkaloids and is not considered palatable to predators, may experience limits on its population in the tadpole stage of its life history; predation and/or competition may be hypothesized in that case.

Two major findings of this study are of particular note, and should be pursued in subsequent studies. They are the differences between the forest and cacao habitats and the pronounced seasonality, for both the herpetofauna and several environmental parameters. The seasonality is even more pronounced in the cacao. I recommend further studies of tropical seasonality, both for theoretical and practical purposes. I hypothesize that increased destruction of the tropics will cause greater seasonality, which must be understood and taken into account in any management of the tropics or theoretical study of tropical succession.

LITERATURE CITED

Abrams, P. 1979. Some comments on measuring niche overlap. *Mathematical Biosciences* 28:357-372.

Albuquerque, E., W, Daly and **B. Witkop.** 1971. Batrachotoxin: chemistry and pharmacology. *Science* 172:995-1002.

Ashton, P. Ecological studies in the mixed dipterocarp forests of Brunei State. *Oxford For. Mem.* 25.

Ashton, P. Speciation among tropical forest trees: some deductions in light of recent evidence. *Biol. J. Linn. Soc.* 1:155-196.

Ballinger, R. Reproductive strategies: food availability as a source of proximal variation in a lizard. *Ecology* 58:628-635.

Berry, P. 1965. The diet of some Singapore Anura (Amphibia). *Proc. Zool. Soc. London* 144:163-174.

Bigger, M. 1976. Oscillations of tropical insect populations. *Nature* 259:207-209.

Birch, D. 1981. Dominance in marine ecosystems. *Am. Nat.* 118:262-274.

Bray, J. and **E. Gorham.** 1964. Litter production in forests of the world. *Adv. Ecol. Res.* 2:101-157.

Buskirk, R. and **W. Buskirk.** 1976. Changes in arthropod abundance in a highland Costa Rican forest. *Am. Mid. Nat.* 95:288-298.

Clifford, H. and **W. Stephenson.** 1975. *An Introduction to Numerical Classification.* Academic Press, New York.

Cody, M. 1968. On the methods of resource division in grassland bird communities. *Am. Nat.* 102:107-147.

Cody, M. and **J. Diamond.** 1975. *Ecology and Evolution of Communities.* Belknap Press, Harvard Univ. Press, Cambridge, Mass.

Connor, E. and **D. Simberloff.** 1979. The assembly of species communities: chance or competition? *Ecology* 60:1132-1140.

Day, J., J. Field, and **M. Montgomery.** 1971. The use of numerical methods to determine the distribution of the benthic fauna across the continental shelf of North Carolina. *J. Anim. Ecol.* 40:93-121.

Denlinger, D. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. *Biotropica* 12:100-106.

Dueser, R. and **H. Shuygart.** 1979. Niche pattern in a forest floor small mammal fauna. *Ecology* 60:106-118.

Ewel, J. 1980. Tropical succession: manifold routes to maturity. *Biotropica* 12:2-7. Supplement: Tropical Succession.

Fitch, H. 1973. A field study of Costa Rican lizards. *Univ. Kansas Sci. Bull.* 50:39-126.

Goodall, D. 1973. Sample similarity and species correlation. *In:* R. Whittaker (Ed.). *Handbook of Vegetation Science, Part V. Ordination and Classification of Comunities.* The Hague, Junk: 105-156.

Gray, L. 1979. The use of psychophisical unfolding theory to determine principal resource axes. *Am. Nat.* 114:695-706.

Green, R. 1971. A multivariate statistical approach to the Hutchinsonian niche: Bivalve molluscs of Central Canada. *Ecology* 52:543-556.

Hall, A. 1969. Avoiding information distortion in automatic grouping programs. *Syst. Zool.* 18:318-329.

Hartshorn, G. 1980. Neotropical forest dynamics. *Biotropica* 12:23-30. Supplement: Tropical Succession.

Heatwole, H. and **O. Secton.** 1966. Herpetofaunal comparisons between two climatic zones in Panama. *Am. Midl. Nat.* 75:45-60.

Heyer, W. and **K. Bewen.** 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. *Ecology* 54:642-645.

Heyer, W. 1976. Studies in larval amphibian habitat partitioning. *Smith. Cont. Zool.* 242.

Holdridge, L. 1967. *Life Zone Ecology.* San José, Costa Rica.

Holmes, R., R. Bonney, and **Pacala.** 1979. Guild structure of the Hubbard Brook bird community: a multivariate approach. *Ecology* 60:512-520.

Hope, K. 1969. *Methods of Multivariate Analysis.* Gordon and Breach, New York.

Hudson, R. 1976. Resource division within a community of large herbivores. *Naturaliste Canadien* 103: 153-167.

Huhta, V. 1979. Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after clear-cutting. *Oecologia* (Berl.) 41:11-23.

Inger, R. and **H. Marx.** 1961. The food of amphibians. Exploration du Parc National de l'Upema. *Inst. des Parcs Nat. du Congo et du Ruandi-Urundi.* Fascicule 74.

Inger, R. and **R. Colwell.** 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. *Ecol. Monogr.* 47:229-253.

Inger. R. 1980a. Densities of floor-dwelling frogs and lizards in lowland forests of Southeast Asia and Central America. *Am. Nat.* 115:761-770.

Inger. R. 1980b. Relative abundances of frogs and lizards in forests of Southeast Asia. *Biotropica* 12:14-22.

Janzen, D. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. *Biotropica* 6:69-103.

Kira, T., H. Ogawa, K. Yoda, and **K. Ogino.** 1967. Comparative ecological studies on three main types of forest vegetation in Thailand. IV. Dry matter production with special reference to the Khao Chong rain forest. *Nat. Life Southeast Asia* 5:149-174.

Lieberman, S. and **C. Dock.** 1982. The leaf litter arthropod fauna of a lowland tropical evergreen forest site (La Selva, Costa Rica). *Rev. Biol. Trop.* 30:27-34.

Lloyd, M., R. Inger, and **F. King.** 1968. On the diversity of reptile and amphibian species in a Bornean rain forest. *Am. Nat.* 102:497-515.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. *Ecology* 36:533-536.

MacArthur, R. 1969. Patterns of communities in the tropics. *Biol. J. Linn. Soc.* 1:19-30.

——. 1970. Species packing and competitive equilibrium for many species. *Theor. Pop. Biol.* 1:1-11

May, R. 1973. *Stability and Complexity in Model Ecosystems.* Princeton Univ. Press, Princeton, N. J.

May, R. 1974. On the theory of niche overlap. *Theor. Pop. Biol.* 5:297-332.

McNoughton, S. and **L. Wolf.** 1970. Dominance and the niche in ecological systems. *Science* 167:131-139.

McVey, M., R. Zahary, D. Perry, and **J. MacDougal.** 1981. Territoriality and homing behavior in the poison dart frog *(Dendrobates pumilio). Copeia* 1981:1-8.

Orloci, L. and **M. Mukkattu.** 1973. The effect of species number and type of data on the resemblance structure of a phytosociological collection. *J. Ecology* 61:37-46.

Pianka, E. 1973. The structure of lizard communities. *Ann. Rev. Ecol. Syst.* 4:53-74.

Pielou, E. 1966. The measurement of diversity in different types of biological collection. *J. Theor. Bio.* 131:131-144.

Savage, J. 1968. The Dendrobatid frogs of Central America. *Copeia* 1968:745-776.

Savage, J. and **S. Emerson.** 1970. Central American frogs allied to *Eleutherodactylus bransfordii:* a problem of polymorphism. *Copeia* 1970:623-644.

Savage, J. 1980. A handlist with preliminary keys to the herpetofauna of Costa Rica. *University of Southern California Publ.* Los Angeles.

Savage, J. and **R. McDiarmid.** 1981. Amphibians and Reptiles of the Osa Peninsula, Costa Rica. Manuscript.

Schoener, T. 1974. Resource partitioning in ecological communities. *Science* 185-27-39.

Scott, N. 1976. The abundance and diversity of the herptetofauna of tropical forest litter. *Biotropica* 8:41-58.

Shannon, C. 1964. A mathematical theory of communication. *Bell System Tech. J.* 27:379-423

Smith, R. 1976. Numerical Analysis of Ecological Survey Data. Ph. D. Dissertation, Univ. of So. Calif., Los Angeles.

Sneath, P. and **R. Sokal.** 1973. Numerical Taxonomy. W. H. Freeman and Co., San Francisco.

Starrett, P. 1960. Descriptions of tadpoles of Middle American frogs. *Misc. Publ. Mus. Zool., Univ. Mich.* 110.

Talbot, F., B. Russel. and **G. Anderson.** 1978. Coral reef fish communities: unstable high diversity systems? *Ecol. Monogr.* 48:425-440.

Talbot, J. 1977. Habitat selection in two tropical anoline lizards. *Herpetologica* 33:114-123.

Talbot, J. 1979. Time budget, niche overlap, inter-and intra-specific aggression in *Anolis humilis* and *Anolis limifrons* from Costa Rica. *Copeia* 1979:472-481.

Toft, C. 1980a. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparision of wetter and drier sities. *Oecologia* (Berl.) 47:34-38.

Toft, C. 1980b. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* (Berl.) 45:131-141.

Toft, C. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *J. Herpetol.* 15:139-144.

Whittaker, R., S. Levin and **R. Root.** 1973. Niche, habitat, and ecotope. *Am. Nat.* 107:321-333.

Wiens, J. 1977. On competition and variable environments. *Am. Sci.* 65:590-597.

Wolda, H. 1978. Fluctuations in abundance of tropical insects. *Am. Nat.* 112:1017-1045.

Wolda, H. 1979. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *J. Anim. Ecol.* 47:369-382.

Young, A. 1979. Arboreal movement and tadpole carrying behavior of *Dendrobates pumilio* (Dendrobatidae) in Northeastern Costa Rica. *Biotropica* 11:238-239.

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