ANURAN COMMUNITIES IN SOUTHERN BELIZE: A TWENTY-MONTH STUDY OF BREEDING ACTIVITY AND RESOURCE USE AT NINE TROPICAL BREEDING SITES

by

Tanya J. Hawley

A Thesis

Submitted in partial fulfillment of the

requirements of the degree -

MASTER OF SCIENCE

College of Natural Resources

UNIVERSITY OE WISCONSIN

Stevens Point, Wisconsin

May 2002

APPROVED BY THE GRADUATE COMMITTEE OF:

Dr. Erlk Wild
Assistant Professor of Biology

Dr. Eric Anderson
Professor of Wildlife

Dr. Hans Schabel
Professor of Forestry

ABSTRACT

Eighty percent of the world's amphibian species exist in tropical areas and many of these species are not well known. The opportunity to study tropical anuran communities over a long period oftime is rare but vital to understanding their ecology. The activity and habitat use of sixteen species of anurans were examined over a period of twenty months, from February 2000 to October 2001, at nine tropical sites in southern Belize. Eight of the nine sites were in the Bladen Nature Reserve (40,350 ha) within pine-savanna and primary rainforest habitat.. The remaining site was in a cattle pasture near the town of Punta Gorda. Visual encounter and vocalization surveys were used to uncover patterns in activity and resource partitioning on temporal and spatial scales. Canopy cover, vegetation height, tree basal height diameter, and vegetation structure were measured at seven of the sites to examine habitat differences.

Breeding activity closely followed annual precipitation and water permanency. Species breeding strategies differed by type (continuous vs. explosive), duration, and season. Spatial partitioning of resources occurred on both macrohabitat and microhabitat levels, by use of different sites and vertical stratification of habitat within sites. These patterns reflected unique strategies of each species, presumaply to minimize competition, allowing many species to breed successfully at the same site. Four species were breeding-habitat generalists, occurring across the range of habitats surveyed in the study. Eight species were specialists, only encountered in either savanna or forest sites. Canopy cover ranged from 0% at the Disturbed Site to over 83% at the Forest Site. Vegetation height was greatest atthe Savanna Site (89.71 ± 4.07 cm (mean ± SE)) and lowest at the Forest Site (0.77 ± 0.41 cm (mean ± SE)). Habitat characteristics such as canopy cover

and vegetation influenced species presence at a particular site based on species specific physiological and morphological tolerances. Vegetation characteristics such as these may be helpful in predicting the effects of disturbance on sensitive species.

Understanding patterns in anuran activity, breeding, and habitat preference can help us to improve monitoring programs that identify population fluctuations including declines. This knowledge is also useful in managing protected areas to preserve sensitive species and in gaining insight into overall ecosystem health.

ACKNOWLEDGMENTS

First, I would like to thank my graduate committee including Dr. Erik Wild, Dr. Eric Anderson, and Dr. Hans Schabel. Each have been extremely helpful and supportive of my work throughout the entire process. Dr. Erik Wild gave many useful editorial comments during the writing of this manuscript. I would also like to thank Dr. Michael Bozek for valuable advice regarding statistical analysis and for his interest in my work. I am grateful for the Student Research Fund at the University of Wisconsin-Stevens Point for providing crucial funding that allowed the project to begin.

I would like to thank the Conservation Division of the Forestry Department, Ministry of Natural Resources of Belize, including Natalie Rosado, John Pinelo, and Earl Codd, for issuing research permits. I also wish to thank Celso Poot and Sharon Matola at the Belize Zoo for allowing me the time and flexibility to conduct my study while continuing my work as an Outreach Educator. In addition, I am grateful to the Peace Corps Belize staff, especially Country Directors Costas Christ and Bill Barbieri for their encouragement, flexibility, and support.

I received valuable advice via email from Dr. Jack Meyer, Dr. Julian Lee, and Dr. Joseph Mendelson III while I was in Belize. In addition, Dr. Steven Brewer graciously offered his time to identify trees at my sites and provided helpful advice on methods to collect data on vegetation characteristics.

I would like to thank Jake and Kelly Marlin for inviting me to visit the Bladen Nature Reserve and for their support and friendship during my fieldwork. I am also grateful to Brian Holland who helped me select a disturbed site and who introduced me to Jose Ramirez, a private landowner. I would like to thank my fellow Bladen herp

enthusiast, Jim Arrigoni, who provided me with companionship during many hammock discussions about the mysteries of frogs, and crucial caffeine fills before long field nights. There are numerous other persons who assisted me in the field, working long hours hunting frogs and doing other, sometimes monotonous tasks. These people include Karin McLennan, Martin Ack, Wil Schmidt, Derrick O'Brien, Nita Odedra, Armando Canti, Vicente Ack, and especially Wilfred Requena and Peter Shol. I appreciate their hard work and know that this final product would not have been possible without their help.

Finally I would like to thank my parents, sisters, grandma, and other family and friends for their patience and unending support during my adventures.

PROLOGUE

As a student in the Masters Internationalist Program of the Peace Corps, I was given the opportunity to conduct this study while serving as a volunteer in Belize from June 1999 - November 2001. During this time my primary job was as an outreach environmental educator in the Toledo District for the Belize Zoo. I was fortunate to have had the flexibility in my work to spend 4 - 5 days each month at the Belize Foundation for Research and Environmental Education, where I was based while conducting my study.

This thesis was written as a complete synopsis of the study I performed in the Bladen Nature Reserve. Since little research had been conducted on anuran communities in southern Belize, it was important to present the data in this comprehensive form. In this manner, this thesis will serve as baseline data on anuran abundance at the study sites in the Bladen Nature Reserve. I intend to publish smaller portions of this separately.

TABLE OF CONTENTS

RESULTS continued

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDICES

INTRODUCTION

Amphibian Diversity and Population Declines

Environments with high annual rainfall usually have a high number of amphibian species (Duellman and Trueb, 1994). Therefore it is not surprising that approximately 80% of the world's amphibian species are found in tropical ecosystems (Pough et al., 1998). At the same time, loss of habitat in tropical countries has occurred at an alarming rate, with many countries currently having only half of the original wildlife habitat (Conservation International, 1990). The primary reason for this loss of habitat is deforestation as a result of subsistence farming (Whitmore, 1990). Deforestation of large tracts of land can directly cause the extinction of vulnerable species.

Indeed mounting evidence indicates that amphibian populations worldwide are in decline (Blaustein and Wake, 1995; Houlahan et al., 2000). Multiple explanations, including acid precipitation (Beattie and Tyler-Jones, 1992; Sadinski and Dunson, 1992), ultraviolet radiation (Blaustein et al., 1994a; Blaustein et al., 1996; Ankley et al., 1998), pathogenic infection (Laurance et al., 1996; Kiesecker and Blaustein, 1997), exotic species introduction (Lannoo et al., 1994; Tyler et al., 1998), toxins (Hecnar, 1995; Ouellet et al., 1997), climatic factors (Pounds and Crump, 19?4; Laurance, 1996), and normal population fluctuations (Pechmann et al., 1991; Blaustein et al., 1994b), have been proposed to explain this trend. Many of these causes are indirect effects of habitat destruction. However, declines have also been noted ~ areas considered pristine, such as with the golden toad *(Bufo periglenes)* which was once abundant at high elevations within the undisturbed Monteverde Cloud Forest Reserve in Costa Rica, but has not been observed since 1989 and is considered extinct (Crump et al., 1992). Some population declines have involved only one species of a community, whereas in other instances many species are undergoing the same changes. Most studies have been unable to find a single cause to explain the population declines (Sarkar, 1996). Many scientists have suggested that several compounding factors may cause a more lethal effect than one acting alone. Frequently, anurans undergoing decline can be identified by common characteristics. For example, frogs undergoing significant population decline in Australia could all be characterized by low fecundity, reproduction in flowing streams, and as habitat spe?ialists (Williams and Hero, 1998). These characteristics provide important clues to herpetologists regarding which species may be vulnerable in the future. It is also recognized that some trends cannot be attributed to anthropogenic impacts but instead can be attributed to natural fluctuations (Pechmann et al., 1991; Blaustein et al., 1994b). These authors stress the importance of long-term studies in order to factor out uncertainties regarding declines.

Little is understood about the extent of amphibian decline throughout Latin America, where an estimated half ofthe world',s amphibians are found (Duellman, 1999). However, at workshops in Latin America in 1999, herpetologists uncovered that population declines have occurred in at least 13 countries (Ypung et al., 2001). Most declines or disappearances took place in remote higWands during the 1980s. A more thorough understanding of species ecology and natural history is needed to improve the design of monitoring studies that are necessary throughout Latin American (Young et al., 2001). Since an estimated 5 - 10% of the amphibians in Central America remain undescribed (Campbell, 1999) and many more species are not well known, it is evident that research is needed throughout the region.

Many anurans are well documented in the Central American country of Belize and three field guides have been written that encompass the anurans of the area (Meyer and Foster, 1996; Campbell, 1998; Lee, 2000). However, five of the 33 known species in Belize were discovered between 1990-1995 and two species have only been documented once in the country (Meyer and Foster, 1996). Besides the field guides, little has been published concerning anuran activity patterns and resource partitioning in Belize. The importance of documenting these patterns is obvious given the proximity of declines of anurans in other Central American countries. Fortunately, a considerable amount of research has been initiated in recent years involving the amphibians of Belize. A five-year monitoring project titled the Maya Forest Anuran Monitoring Program (MAYAMON), first initiated by the Belize Working proup of the Declining Amphibian Populations Task Force (DAPTF), began in 1997 at sites in Belize and then grew to include sites in southern Mexico and the Peten of Guatemala in 1998 (Meyer, 1997). The goal of this project is to provide baseline data on common anurans by conducting vocalization surveys during the months of June to October each year (Meyer, 1997). In addition, a project examining population dynamics, reproduction, and environmental requirements of anurans started in 2000 at LasCuevas Resea;rch Station in the Chiquibul Forest Reserve (Gardner et aI., 2001). These projects will add much to our understanding of natural population fluctuations of anurans in Belize.

Community Structure

Species distributions reflect unique patterns of history, geography, environmental tolerances, and resource use (Cormell, 1975; McNaughton and Wolf, 1979). These distributions then determine the species that interact through predation and competition on a community level (Toft 1985; Welborn et al., 1996). Anuran species partition the available resources in a habitat on both temporal and spatial scales in order to minimize competition (Crump, 1971). Therefore, the description of amphibian communities requires the definition of many factors acting simultaneously (Toft, 1985). These factors include both biotic and abiotic variables and ecologists have warned of the danger of oversimplifying a community by concentrating on one or two variables instead of looking at interactions between many (Dunson and Travis, 1991). To complicate anuran community structure further, we must be aware that different populations ofthe same species may demonstrate different dynamics (Lawton, 1999) based on the unique conditions present in a certain habitat.. Therefore attempts to generalize community structure can be very difficult (Lawton, 1999). Regardless, we cannot allow this to detract from the value of studies that examine species dynamics and interactions, since this is our only way to attempt to understand the complexities.

Studies by Crump (1971), Duellman (1978), Creusere and Whitford (1976), Strijbosch (1980), Aichinger (1987), Gascon (1991), Donnelly and Guyer (1994), Wild (1996), Eterovick and Sazima (2000), and Vonesh (2001) use resource partitioning to describe anuran adult and/or tadpole communities. Each oqhese works attempts to describe the community with regard to use of habitat characteristics on temporal and spatial scales. These studies represent some of the most comprehensive work completed on anuran communites and similar research is needed including more anuran species and other regions of the world.

Species Activity

Anurans differ in activity on both temporal and spatial levels (Crump, 1971; Duellman, 1978; Aichinger, 1987; Donnelly and Guyer, 1994), and individuals of the same species may have very different activity patterns at different locations. It is important to recognize and understand these influences on a species behavior when monitoring populations. These patterns are especially obvious when species are breeding.

The temporal level of anuran activity, especially timing of reproduction, is highly influenced by rainfall in tropical environments (Crump, 1971; Aichinger, 1987; Gascon, 1991; Donnelly and Guyer, 1994; Duellman and Trueb, 1994; Wild, 1996; Eterovick and Sazima,, 2000). Since many anurans are tied to water for reproduction, their breeding efforts are often confined to the rainy season, especially in locations with a marked dry season. Temporary pools where many species breed often only fill with water after several rainfalls.

Temporal differences in activity are also evident from the different modes of breeding. These include two distinct temporal patterns of breeding, explosive and prolonged patterns, with many variations along a continuum between them (Wells, 1977). Species are also distinct in their season of breeding, some br~eding exclusively in the dry season, some exclusively in the wet season and others in both seasons. Most likely, the amount of time a species spends breeding is determined by physiological constraints, interspecies interactions, and consequently evolutionary adaptation over time. On an even finer level, anurans are found to avoid temporal overlap in calling within the same site (Eterovick and Sazima, 2000; Gardner et al., 2000). This may serve to avoid competition for perch sites or to avoid confusion between species of similar size and calls (Eterovick and Sazima, 2000).

Activity will be influenced by hydroperiod on a spatial level. Individuals of the same species may breed at different times based on water availability at different sites. Crump (1971) and Aichinger (1987) found that some species would alter their breeding concentration from permanent ponds to temporary sites as the wet season progressed. Species presence at a breeding site can be highly variable due to changes in habitat availability and quality (Alford and Richards, 1999).

Anurans also use vertical height to partition activity on a spatial level. Perch heights vary interspecifically (Donnelly and Guyer, 1994; Eterovick and Sazima, 2000), promoting the partitioning of resources in space if twp or more species with similar requirements are breeding at the same time.

Habitat

Species are limited by certain physical and biological characteristics and this results in the range of habitat in which they occur, or in other words their niche (Hutchinson, 1957). This may result in confining a species to a small range where these habitat characteristics exist. These specialists occupy a narrqw niche and often have a small population size because the carrying capacity ofthe specialized environment for that species is smaller than that for a generalized species (Crump, 1971). Typical characteristics of generalist species, on the other hand, are that they are common and have wide ranges (McNaughton and Wolf, 1979). Usually, species with broad niches are stronger competitors than those with narrow niches (Prince, 1984).

Nearly all anuran species would fit the general definition of the term specialist. Prince (1984) explained that specialists are usually small in size, use resources that can be narrowly defined in time and space, have a low dispersal ability, large source of available resources, and are often limited by time. However, within the group of anurans, species that are even more characteristic of these traits can be identified.

Species with a small range and small population density are at most risk of extinction from proximate causes (Lawton, 1995). Consequently, specialists are most often the species that become a concern for conservation (Primack, 1993). They are usually more sensitive to environmental changes and more prone to extinction; therefore, they may be classified as indicators of environmental health (Williams and Hero, 1998). Since amphibians have often been said to be indicators of imbalance within ecosystems due to their unique life history and physiology (Blaustein and Wake, 1995; Phillips, 1990), the role of anuran specialists as indicators may be especially deserving of our attention.

Herpetologists have commonly measured many environmental variables in attempt to define amphibian distributions and to interpret population change (Lips et al., 2001). Typically, combinations of canopy cover, vegetation ,type and height, water depth and temperature, number of trees, air temperature, rainfall, and humidity are measured (e.g., Gascon, 1991; Wild, 1996; Eterovick and Sazima, 2000; Pearman, 1997). In a Michigan study, forest canopy cover and pond hydroperiod were found to be the most influential variables in describing amphibian distributions (Skelly et al., 1999). These two variables can be an effective way to characterize patterns in community composition (Wemer and Glennemeier, 1999). Hydroperiod was also strongly correlated with community structure and diversity of amphibians in South Carolina bays (Pechmann et al., 1989). This is to be expected since hydroperiod represents the maximum limit on development time for most anurans (Welborn et al., 1996). In addition, hydroperiod also determines the type and abundance of predators in aquatic systems (Heyer et al., 1975). In ponds with a long hydroperiod, predators may become established and predation may play a large role in tadpole survival; however, in temporary pools intra- and interspecies competition may play a larger role (Heyer et al., 1975).

Canopy cover plays an important role in regulating abiotic factors such as temperature and humidity within a habitat (Hubbell and Foster, 1986). A closed canopy may act as a more predictable environment in contrast to a canopy with many gaps. Canopy gaps can result in an environment with high~r light intensity and consequently more understory drying due to increased soil and air temperature and lower humidity than the surrounding forest (Hubbell and Foster, 1986). In addition, Werner and Glennemeier (1999) found dissolved oxygen demand to be high in closed canopy ponds due to accumulation of leaf material.

Hydroperiod and canopy cover are easily measured and can lead to many insights concerning species presence in a habitat. Indeed, changes in species composition can be a direct result of natural forest succession (Werner and Glennemeier, 1999). Therefore, collection of data describing the habitat where a species is found is an important addition to monitoring studies. Awareness of these factors can help explain some species population declines or disappearances from sites.

Objectives

Southern Belize is the least studied region of the country although it is also the most diverse, with records for 29 of the 33 species known from the country (Lee, 2000). In addition, it is the region where two species have only been observed on one occasion (Meyer and Foster, 1996; Lee, 2000). The pine-savanna habitat of southern Belize has not been thoroughly studied nor has a study examined specific vegetation attributes of the environment in relationship to anuran species presence. Furthermore, none of the current anuran monitoring projects in Belize are examining year-round patterns of species activities. The paucity of data in these areas led me to develop a project with the following objectives.

The objectives of this research were to: 1) investigate and census anuran species richness and abundance in different habitats of southern Belize; 2) explore year-long temporal and spatial distributions of species activity; and 3) examine community structure and habitat use of anuran species.

METHODS

Study Sites

The study sites were located in the Toledo District of southern Belize and all except one were in the southeast part of the Bladen Nature Reserve (BNR) (Fig. 1). BNR was officially set aside as a reserve in 1977 and has a total area of 40,350 hectares. Scattered logging occurred within the southeast region of the reserve until 1970; however, the reserve is said to encompass the most pristine rainforest in Belize. In Belize, nature reserves have the highest level of protection, are designated especially for wildlife conservation, and are only officially open to researchers with a permit.. However, there is no management plan or official presence within BNR and as a result subsistence hunting continues.

The climate of Belize is described as subtropical to tropical (Meerman and Sabido, 2001). The annual mean maximum temperature ranges from 28° C to 33° C and mean minimum temperature ranges from 16° eto 24° C (Meerman and Sabido, 2001). Precipitation is greatest in the south of the country,with approximately 4,000 mm per year (Meerman and Sabido, 2001). The majority of precipitation falls from June to October, with a distinct dry season occurring from November to May.

Sites within BNR were located along and off of a din road that originated on the Southern Highway and terminated at a crossing on the Bladen River adjacent to the Belize Foundation for Research and Environmental Education (BFREE) (Fig. 1). There was very little traffic on this road, usually only one four-wheel vehicle weekly. During the wet season the road was inundated with water in many portions and very difficult to pass.

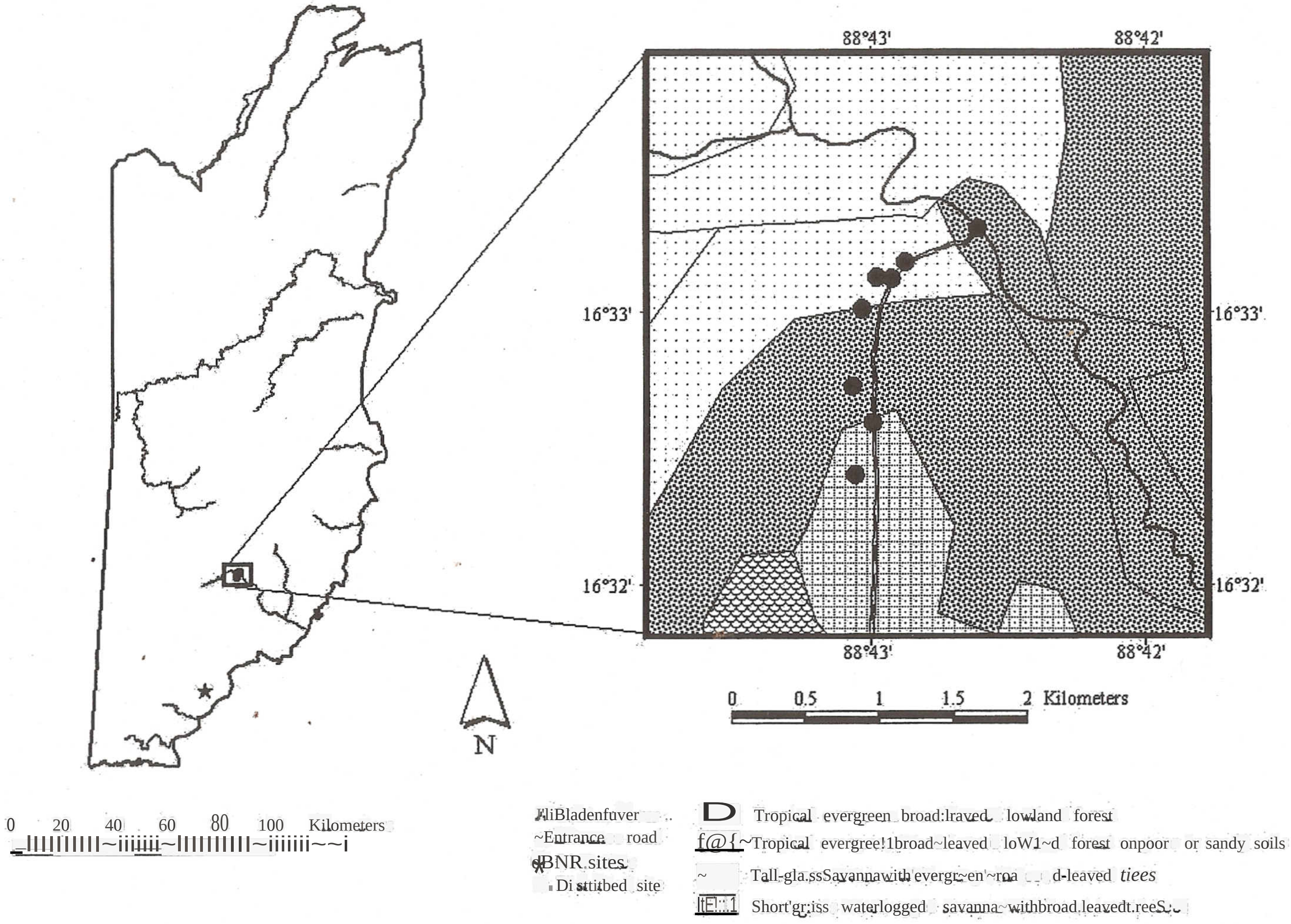


Figure 1. Map indicating study sites in southern Belize. Detail of BNR ecosystems was adapted from the Belize ecosystems map (Meerman and Sabido, 2001).

One forest and one savanna site were selected during the dry season (February 2000) to be intensively sampled. Effort was made to select sites that appeared suitable for anuran breeding activity. When the wet season began in May 2000, additional sites were selected based on the activity and breeding of anurans. A total of eight sites, three on the entrance road, four off the road, and one at the crossing of the Bladen River, were regularly surveyed. These sites ranged from primary tropical evergreen broadleaf lowland forest to short-grass savanna (Meerman and Sabido, 2001) at elevations of30-61 m (Fig. 1). The forest was 30 - 40 m tall and tree diversity (individuals> 10 cm DBH) was 80 - 100 species with 330 - 360 individuals/ha (Brewer and Rejmanek, 1999).

An additional location near the village of Forest Home, Toledo District was surveyed on an irregular basis during the study. This\locality was a cattle pasture with surrounding secondary growth forest and represented a "disturbed" study site.

Amphibian Sampling

Amphibian sampling occurred during twenty months, from February 2000 to October 2001, excluding March 2001.. The BNR sites were surveyed during a two to five day period each month. Each site differed in sampling effort, which will be described further in the "Site Descriptions" section. By July 2000, all ~ight sites in the BNR were visited at least once per month, although most were visited two to four times each month. The Disturbed Site was not visited as regularly as the sites in the BNR, yet these data are included to serve as a comparison between disturbed and undisturbed locations.

Nocturnal visual encounter surveys (Crurnp and Scott, 1994) were intended to be the main method of data collection during the study; however, it was realized during the first rains that this would result in the presece of several species being overlooked. For example, a species such as *Leptodactylus labialis* calls from underground burrows and would not usually be documented except by calling surveys. Consequently, nocturnal calling surveys were conducted along a 100 m transect, located through the center of each site. These call surveys became the main source of data on species presence and abundance at each site. Audio transects such as these are regarded as accurate in producing estimates of the relative abundance of calling males and in determining the spatial boundaries of species (Zimmerman, 1994). The number of calling males of each species was estimated and recorded as an index of 1 to **4,** following the protocol used in the MAYAMON research so that nationwide comparisons can be made (Meyer, 1997). A calling index of 1 indicates that 1 - 5 individuals were calling; 2 indicates 6 - 20 individuals; 3 indicates 21 - 50 individuals; and 4 inqicates over 50 calling individuals. Calling surveys in excess of three minutes rarely result in the identification of new species (Shirose et aI., 1997); however, surveys in this study were conducted for a minimum often minutes. Surveys began at approximately 20:00 hours each night and continued until 23:00 or 24:00 hours, corresponding with the time period of greatest frog calling (Pearman et aI., 1995; Stewart, 1995; Marsh and Pearman, 1997).

Although the main emphasis of data collection were the vocalization surveys, visual encounter surveys (Crump and Scott, 1994) were continued at each site along the same 100 m transect.. The transect was walked during each nocturnal call survey and each individual encountered within 2 m of the line was identified to species. An attempt was made to walk the entire transect, but this did not always occur depending on the abundance of anurans and time. When an individual was spotted, it was noted with respect to hour, substrate type, and activity. Categories to distinguish substrate were based on site characteristics. Activity notes included whether the species was calling, breeding, or simply observed.

Systematic diurnal transect sampling was conducted for one year to ensure that no species were being overlooked. The same methods were employed as that for the nocturnal transect surveys. In addition, informal diurnal searches during the entire study were completed and often confirmed egg presence after nights of active breeding. Easily identified tadpoles were also noted at each site.

Perch heights of species of Hylidae were recorded on occasion during both years of the study. The height was measured to the nearest cm with a standard yardstick. Heights over 1 m were estimated by the observer and only two species were found with regularity at these heights.

Opportunistic sightings of species in route to the sites in BNR were noted throughout the study. The same methods employed for the sites in BNR were used at the Disturbed Site. Global Positioning System coordinates were recorded at each site and photos of each site and anuran species were taken periodically throughout the study. Representative recordings of vocalizations during active nights each year were taken for most species. To maintain standardization in technique, the same person conducted all surveys with the assistance of a field assistant.

Environmental Variables

Climatic and habitat variables were collected in order to account for differences in species richness and abundance throughout the year and between sites. Precipitation and maximum and minimum temperatures were recorded daily at BFREE and at the Disturbed Site by standard methods. Temperature and percent humidity were recorded with a battery operated thermohygrometer at 1 m above the ground in the forest and savanna during each survey night. Water depth (to the nearest cm) was measured monthly at a stationary post in the center of the Forest Site and Savanna Site throughout the study. At other sites, water presence was recorded each month and depth was recorded monthly during the 2001 wet season.

Collection of habitat variables took place at seven of the nine sites during the months of August to October 2001. Unfortunately Hurricane Iris (Meerman, 2001) substantially altered the habitat within most sites on 12 October 2001, before habitat variables were collected at the remaining two sites. The habitat variables measured included canopy cover, number of trees, tree diameter at basal height (DBH), herbaceous vegetation height, vegetation structure, and vegetation types.

Methods used by Gascon (1991) were employed to collect the data on vegetation structure. The methods were originally developed by Hubbell and Foster (1986) and were modified to fit the needs of this study. A 20 x 10 m area, divided into a grid at 2 m intervals, was measured in each site. The area was selected purposefully to surround the pool within the site and an attempt was made to contain vegetation representative of the site as a whole. Three measurements of vegetative cover were taken at each 2 x 2 m intersection, including the vegetative stratum between 0 to 2.5 m, 2.5 to 5.0 m, and 5.0 to 30.0 m. A value of 0 to 3 was given, corresponding to 0 – 25, 25 – 50, 50 – 75, and >75% vegetation coverage. These values were determined by placing a stick on the grid intersection point and estimating the percent of the stick length that came in contact with vegetation. A paper roll opening was divided into four equal parts with a string and looked through to estimate percent canopy cover. Each grid intersection was given a value of 0 – 3 based on the same percent coverage as the vegetation structure methods. Herbaceous vegetation height and water depth were measured to the nearest cm at each intersection point. In addition, a map was made of each site indicating the general types of vegetation contained within each grid square.

Data Analysis

The discovery of new species with time was analyzed to evaluate sampling success in each site. If the number of new species observed reaches an asymptote, it may be concluded that within the limitation of the methods used, all the species present in the area have been found. In addition, the minimum common number of field days was used to compare across sites with different sampling effort to evaluate species richness.

Mean values for monthly temperature and precipitation taken at BFREE and at the Disturbed Site were calculated and examined graphically. A mean value was also calculated for temperature and humidity measurements collected during survey days and nights of the first study year at the Forest Site and Savanna Site. These values were evaluated graphically to examine differences in abiotic factors from day to night and between sites.

Correlation between monthly precipitation patterns and the number of species observed and calling was analyzed with Pearson's correlation coefficient (Zar, 1996). The correlation between the number of species observed and calling was also analyzed in this manner.

The highest calling index and greatest number of visually observed individuals during any one monthly survey were used to analyze species activity on a temporal scale. Observations of breeding activity found during any monthly survey were examined.

Spatial patterns were evaluated by examination of species richness totals and the number of species visually observed or calling monthly at each site.

Mean perch height was calculated for each species of Hylidae to examine vertical partitioning of the habitat. Analysis of variance (ANOVA) and Tamhanes post-hoc test were used to test for differences in mean perch height between species (Zar, 1996). The data were tested to confirm that the assumptions of normality and homoscedascity were met.

A mean value for each habitat variable was calculated for each site. The correlation between variables was analyzed with Pearson's correlation coefficient (Zar, 1996) and uncorrelated variables (canopy cover and vegetation height) were analyzed further for differences among sites. These variables were compared by a nonparametric Kruskal-Wallis test (Zar, 1996), since the data did not meet the assumptions of homoscedasticity and normality, and Tamhanes post-hoc test was used to test for significant site differences.

Species habitat preferences were analyzed by calculating a mean value of canopy cover and vegetation height, including only the sites where the species was present. This gave a value that can be interpreted as the niche space for the species, representing its habitat range with respect to the variables. This value then was recalculated only including sites where the species was encountered in breeding activity during more than one month of the study. Breeding activity in this case was defined as any observation of vocalizing individuals, amplexus, eggs, or tadpoles. This calculation provided a better indication of the breeding niche space for the species. These values were plotted with their respective standard errors to examine niche space and species associations.

Coefficient of Jaccard similarity values (Krebs, 1999) were calculated (Jaccard's coefficient = c/(a+b-c), where a = number of species in site A, b = number of species in site B, and c = number of species present in both sites A and B, to evaluate the similarity in species presence among sites. The coefficient ranged from 0.0 if the sites had no species in common to 1.0 if the sites had identical species present..

RESULTS

Site Descriptions

Bladen River Crossing Site

The Bladen River was surveyed at the crossing leading to BFREE and along 50 m on either shore. Surveys were conducted during each month of the study. The north shore of the river had steep, eroded banks with little vegetation except for trees present approximately 2 - 3 m above the water level.. The south shore was a sandy beach that gradually sloped toward the water. The substrate of the river was comprised oflarge rocks over sand.

A substantial flood on 17July 2000 temporarily increased the width of the river from a typical 20 m at the crossing to over 300 m and caused noticeable changes to the riverbank. The north side had significant sediment erosion and fallen trees. The south side became even more gradual with a longer sandy bank.

Base of Hill Site and Forest Entrance Site

The Base of Hill Site and Forest Entrance Site were located on the entrance road. The Base of Hill Site measured approximately 100 x 10 m, whereas the Forest Entrance Site measured approximately 200 x 15 m. They were about J00 m from each other. Surveys began at the Base of Hill Site in April 2000 and at the Forest Entrance Site in February 2000. At both sites surveys continued until the study ended in October 2001..

Both sites fall under the classification of tropical evergreen broadleaf lowland forest over rolling calcareous hills, as described by Meerman and Sabido (2001). Yet there was disturbance within each site since they were located along the road. Half of each site consisted of open pools of standing water in tire tracks and contained little vegetation. The other half of each site was filled with grasses, wild cocoa, shrubs, and heliconia amongst the pools of water. Most of the vegetation measured 0 - 1.5 m in height, resulting in little light reaching the ground. However, at the Forest Entrance Site the vegetation was periodically cut in order to maintain the road. There was a gap in the vertical vegetative structure at both sites from 1.5 m until the canopy, which began at approximately 15 m at the Base of Hill Site and 10 m at the Forest Entrance Site, and reached to over 30 m at both sites. There were openings in the canopy, especially in the center of the sites.

Water was present in both sites throughout the year, except for one brief drying period in April 2000 and additionally during March 2000 at the Base of Hill Site. The water depth decreased to less than 3 cm during the dIJ season and increased to over 50 cm at the Base of Hill Site and 65 cm at the Forest Entrance Site during the wet season. These sites proved to be excellent breeding areas for many species, but it seemed likely that most species retreated into the surrounding forest by day, since there was little cover for escape directly within the sites.

Forest Site

The Forest Site was situated at the base of a limeston,e hill approximately 100 m from the Forest Entrance site. Surveys began in February 2000 and continued until the termination of the study in October 2001. No nocturnal surveys were conducted from August to October 2001..

The site was considered tropical evergreen broadleaf lowland forest over rolling calcareous hills (Meerman and Sabido, 2001) with a tree density of330 - 360 individuals/ha, tree diversity of 80 - 100 species/ha, and tree heights reaching 30 - 40 m

(Brewer and Rejmanek, 1999). The cohune palm *(Orbignya cohune)* was common in the understory, as well as various heliconias, ferns, shrubs, and other palms. A depressed area (30 x 15 m) acted as a temporary pool for the site. It filled with water after several days of continuous rain and then emptied within a few hours to two days. There was a very efficient drainage system, perhaps of porous limestone or a cavern under the hill. The greatest depth reached by the pool was 33.5 cm on 24 September 2001 after heavy rains. Leaf litter (1 - 7 cm in depth) was present in throughout the site and consisted of fallen leaves, sticks, and branches. Overhanging vegetation was not prominent in the form of vines but was present as trees limbs (3 - 4 m above ground). The canopy was mostly closed and little light reached the forest floor.

Forest Pool Site

The Forest Pool Site was located off ofthe entrance road in tropical evergreen broadleaflowland forest over rolling calcareous hills (Meerman and Sabido, 2001). Surveys began in July 2000 and continued until November 2001 in an area that measured approximately 100 x 10 m. This site was a true temporary pool, filling and maintaining water only after continuous periods ofrain. When observations began on 12 July 2000, the pool had already filled and it maintained water through t1}ewet season. It was found dry on 19 December 2000. In 2001, the pool was not filled until surveys in July (20 July 2001) and it maintained water after the study ended in October 2001. The pool extended to over 80 x 15 m during the height of the wet season. The center of the site reached a maximum depth of 24 cm measured on 25 September 2001, although other areas of the pool reached depths of up to 50 cm. The mean depth from measurements taken on surveys during July to October 2001 was 19.9 ± 3.9 cm (mean ± SD).

One feature unique to the Forest Pool Site was the great amount of overhanging vegetation, mostly in the form of woody vines. This provided abundant cover and perching sites for anurans to about 5 m above the water. There was not a great amount of herbaceous growth or grasses within the site due to the closed canopy. Much of the vegetation was either shrubs or trees. There was a heavy layer of debris in the water, consisting of leaf litter, logs, and sticks. The canopy was mostly closed and extended to only about 25 m, with occasional small gaps where light penetrated the forest floor.

Transition Pool Site

The Transitional Pool Site was located off of the entrance road in transitional habitat between the broadleaf forest and pine-savanna habitats. The site was tropical evergreen broadleaf lowland forest over poor or sandy soils (Meerman and Sabido, 2001). Surveys began at the site in June 2000 and continued throughout the study period. The vegetation within the site consisted of a mix of pine-savanna and forest species. Pine trees *(Pinus caribaea)* and palmettos were present along with small broadleaf trees and shrubs. Overhanging vines were abundant throughout the site. The canopy measured only 20 – 25 m in height but provided nearly complete cover with little light penetrating to the forest floor.

The pool within the site was temporary with water present during surveys in July to November 2000 and July 2001 until the study ended. During 2001, the pool depth reached a maximum of 36 cm on 27 September and the mean depth was 28 ± 11.5 cm (mean ± SD) during surveys from July to October.

Savanna 100 m Site

The Savanna 100 m Site was located on the entrance road in short-grass savanna with needle-leaved trees as described by Meerman and Sabido (2001). Surveys began at the site in May 2000 and continued until the study ended. The site measured approximately 100 x 10 m and was regularly disturbed by vehicle traffic once per week.

This site maintained water throughout the year, with a maximum depth of 36 cm recorded on 27 September 2001. The vegetation consisted of grasses, small shrubs, and other herbaceous plants. The vegetation was very dense and high (up to 1.5 m) on the edges of the site, but sparse and patchy in the middle (0 – 50 cm). Pine trees *(Pinus caribaea)* were present in the surrounding area; however, by the end of the study many trees had died due to the pine bark beetle infestation. Canopy cover was minimal, only filled by pine tree crowns.

Savanna Site

The Savanna Site was located about 200 m off of the entrance road and measured approximately 100 x 10 m. The habitat fell into the short-grass savanna with needle-leaved trees category described by Meerman and Sabido (2001). Surveys began in February 2000 and continued until the study ended.

This site was centered upon an old logging road that filled with water during the wet season. In 2000, the pool was filled with water when surveyed on 22 June and maintained water until it was found dry during a survey on 19 December; in 2001, water was not present until a survey on 31 July and it persisted until the study ended. The water level reached a maximum of 30 cm in October 2001, with a mean depth of 21.6 ± 7.4 cm (mean ± SD) during the six months of the rainy season in 2000. On either side of the center pool, the site was filled with dense grasses to over 150 cm in height and herbaceous plants. Canopy cover in the site consisted of the crown of a pine or craboo tree at about 20 m. Fires were common during the dry season in this area of the BNR. During April 2000, fire consumed the site, yet new grasses were growing by May. Fires did not reach the site during the 2001 dry season.

Disturbed Site

The Disturbed Site was located in a cattle pasture on the edge of Forest Home Village near the town of Punta Gorda, Toledo District. Meerman and Sabido (2001) described the habitat as shifting cultivation and/or unimproved pasture. This site was visited less regularly than the BNR sites, with only six visits during the study.

The center area would fill with 10 - 20 cm of water after several continuous rains. No trees were present directly within the study area so the canopy was completely open. Cattle selectively ate the grasses and herbaceous vegetation, so while most vegetation was eaten down to a couple centimeters in height, other shrubby growth was slightly taller. A couple large trees were present within a short distance and may have served as habitat for many anuran species, especially treefrogs (Hylidae).

Anuran Sampling Success

All of the following results will refer to the eight sites in the BNR (i.e., not Disturbed Site) unless otherwise specified. Total species richness of the BNR sites was 16 species in six families (Table 1). In the Disturbed Site, total species richness was seven in four families (Table 2). Not only did BNR sites have higher species richness and a greater number of families than the Disturbed Site but there were also almost three times as many hylids in the BNR sites. All species encountered had a life cycle with a

Table 1. Overall anuran species richness in the Bladen Nature Reserve study area from February 2000 - October 2001.

Family	Species
Bufonidae	*Bufo marinus*
	Bufo valliceps
Leptodactylidae	*Leptodactylus labialis*
	Leptodactylus melanonotus
Hylidae	*Agalychnis callidryas*
	Hyla ebraccata
	Hyla loquax
	Hyla microcephala
	Hylapicta
	Scinax staufferi
	Smilisca baudinii
	Smilisca cyanosticta
Microhylidae	*Gastrophryne elegans*
Ranidae	*Rana berlandieri*
	Rana vaillanti
Rhinophrynidae	*Rhinophrynus dorsalis*

Table 2. Anuran species richness at the Disturbed Site.

Family	Species
Bufonidae	*Bufo marinus*
	Bufo valliceps
Leptodactylidae	*Leptodactylus labialis*
Hylidae	*Hyla microcephala*
	Scinax stauffiri
	Smilisca baudinii
Ranidae	*Rana berlandieri*

tadpole stage and required water for breeding activity and tadpole development.

The number of total species in the BNR reached an asymptote at n = 25 field days; however, one more species was observed on field day 59 (Fig. 2). Since sites did not have equal sampling effort, species richness can be compared at the minimal common sampling effort of n = 26 field days. The Forest Entrance Site and Base of Hill Site had the highest species richness of all sites, with 12 species at 26 field days of sampling. The Bladen River Crossing Site, Forest Site, and Savanna Site had the lowest species richness with five species. The Forest Pool Site, Transition Pool Site, and Savanna 100 m Site each had 10 species at n = 26 field days. The Disturbed Site was not included on this figure because only six surveys were conducted in the site.

Temporal Distribution of Anuran Activity

BNR was characterized by a distinct wet and dry seasonal cycle. Typically the dry season lasted from November to April and the wet season lasted from May to October. Total annual precipitation was 2637.0 mm during 2000. The driest months of the study were March and April, with 55.2 mm of precipitation in 2000 (2% of the year's total) and 90.6 mm in 2001 (Fig. 3). The rainy season, May to October, had 87% (2295.4 mm) ofthe annual precipitation in 2000. In 2000, June, July?and August each had over 400 mm of rainfall each month. However, in 2001, only August and September had over 400 mm of rainfall. Precipitation at the Disturbed Site was higher than at BFREE almost every month (Fig. 3). It is important to note that during this study the wet season began and ended about one month earlier than the previous three years. May had over 200 mm of precipitation during 2000 and 2001; however, in the three years prior only 36.3 ± 9.3

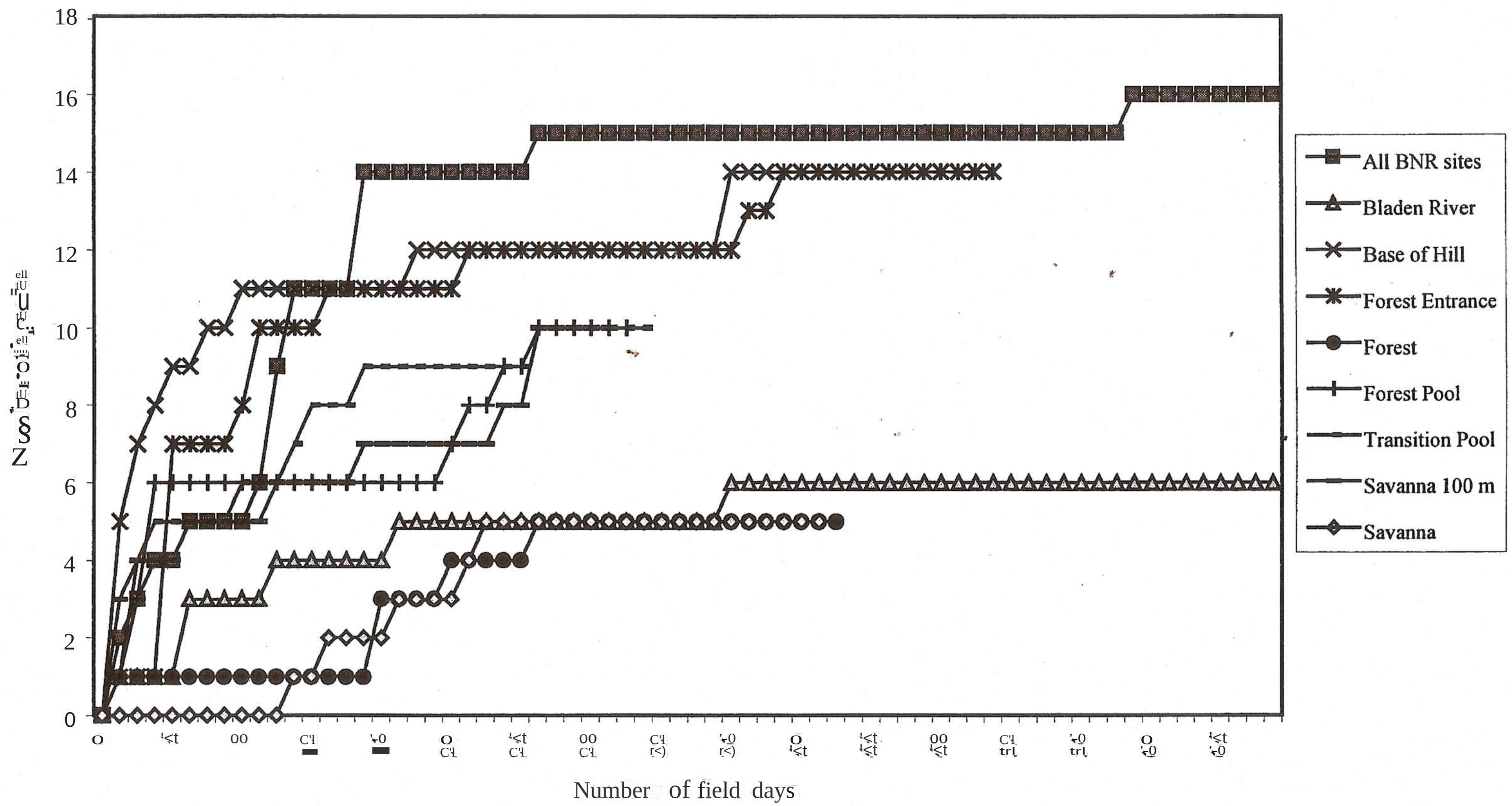


Figure 2. Species discovery curves at the eight study sites within BNR.

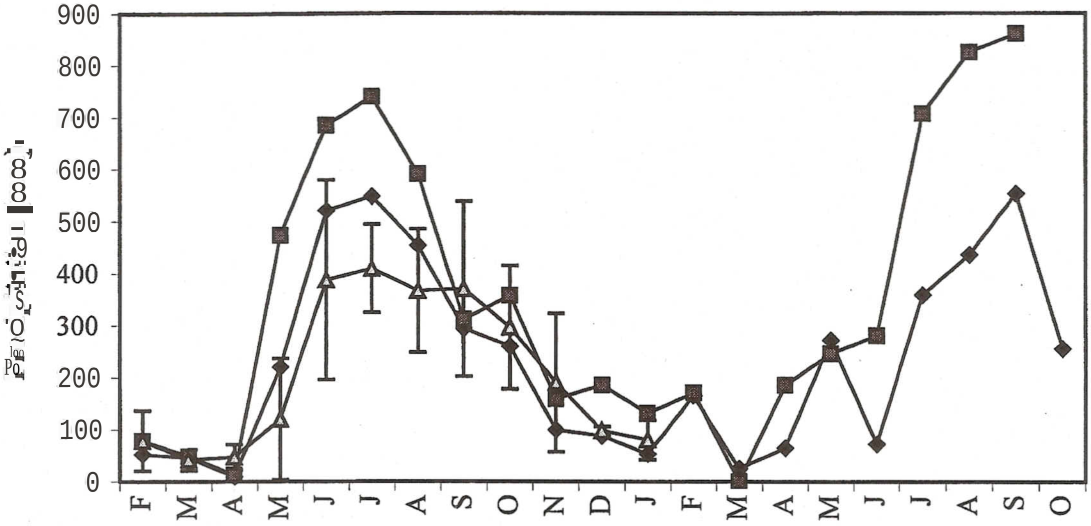


Figure 3. Monthly precipitation totals collected at BFREE (diamonds) and the Disturbed Site (squares) from 2000 - 2001. Triangles represent mean precipitation per month (± SD) at BFREE from 1997 - 2001.

mm (mean ± SD) was reported for May (Fig. 3). June 2001 was an abnormal month, with only 72.5 mm of precipitation, whereas during the four previous years an average of 466.2 ± 88.0 mm (mean ± SD) was reported for the month. From 1997 – 2001, greater variation in precipitation was present during the wet season months in comparison to dry months (Fig. 3).

Monthly maximum and minimum temperatures reached their lowest values in January or Feburary and highest values in April, all dry season months (Fig. 4). During the wet season, mean monthly temperatures were less variable. Temperature at the Disturbed Site followed similar patterns but showed greater variability between maximum and minimum than temperatures recorded at BFREE almost every month, reflecting the lower predictability in its environment.. In addition, temperatures at the Disturbed Site reached a higher maximum value every month.

There was greater day to night variation in relative humidity and temperature in the Savanna Site in comparison to the Forest Site (Fig. 5 & 6). During the day the temperature in the Savanna Site was very high, often exceeding 30° C, while humidity was higher at night. Humidity was typically higher by day and night during the wet season than during the dry season in both sites.

Monthly total precipitation over 200 mm represents a threshold in the number of species calling, reflecting the increase in anuran activity during the wet season (Fig. 7). The outlier data point, representing 72.5 mm precipitation and seven species calling, occurred during June 2001, an unusually dry month after the start of the wet season. Besides this month, only one or two species called during months with less than 200 mm precipitation.

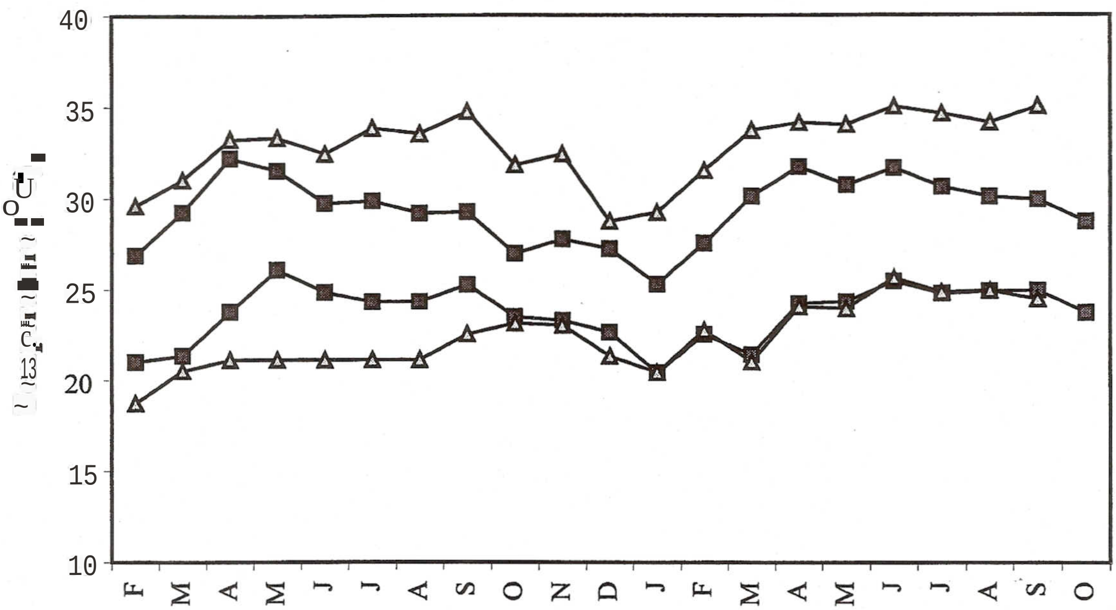


Figure 4. Maximum and minimum mean monthly temperatures collected at BFREE (squares) and the Disturbed Site (triangles) from 2000 - 2001.

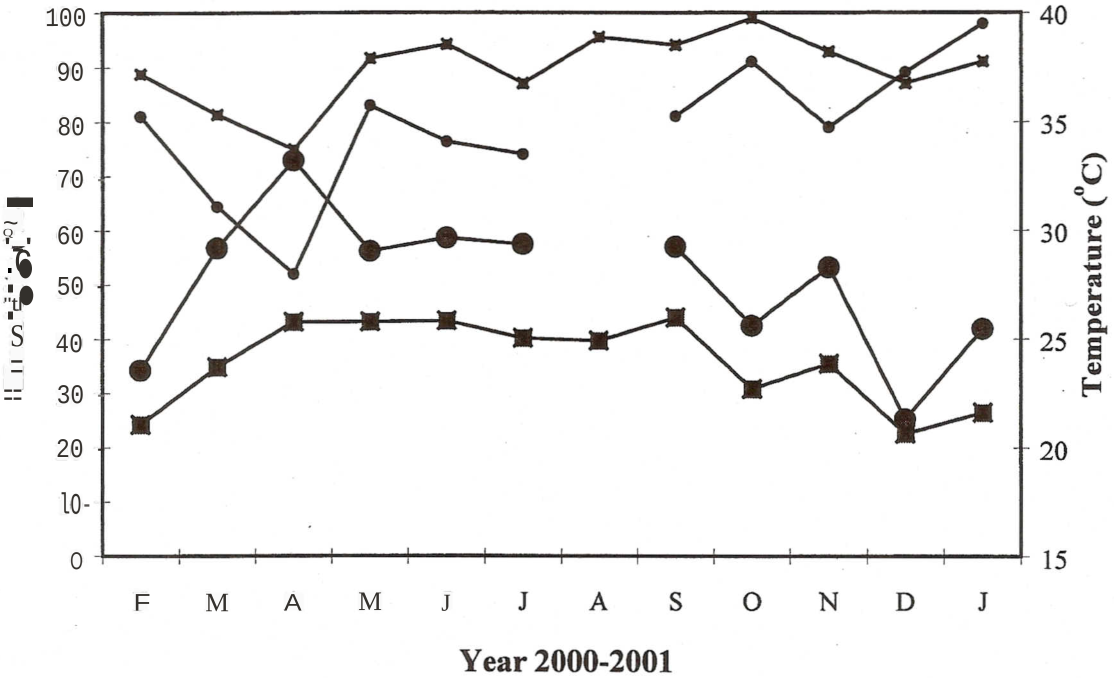


Figure 5. Variation in temperature and humidity at the Forest Site. Small data points indicate humidity and large data points indicate temperature; circles indicate AM and squares indicate PM.

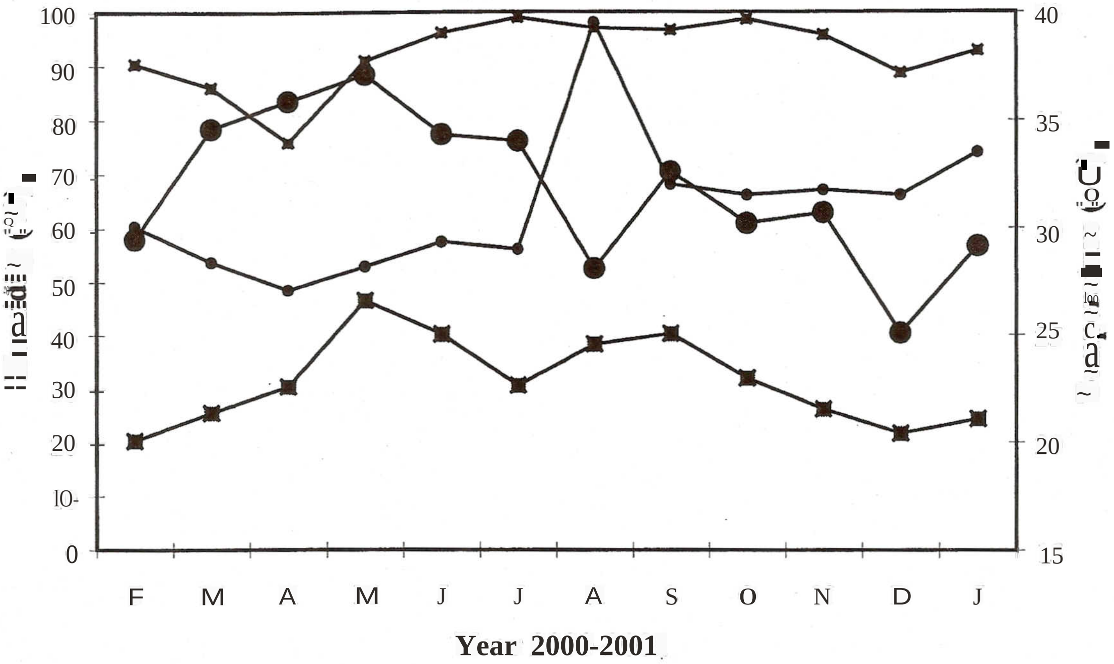


Figure 6. Variation in temperature and humidity at the Savanna Site. Small data points indicate humidity and large data points indicate temperature; circles indicate AM and squares indicate PM.

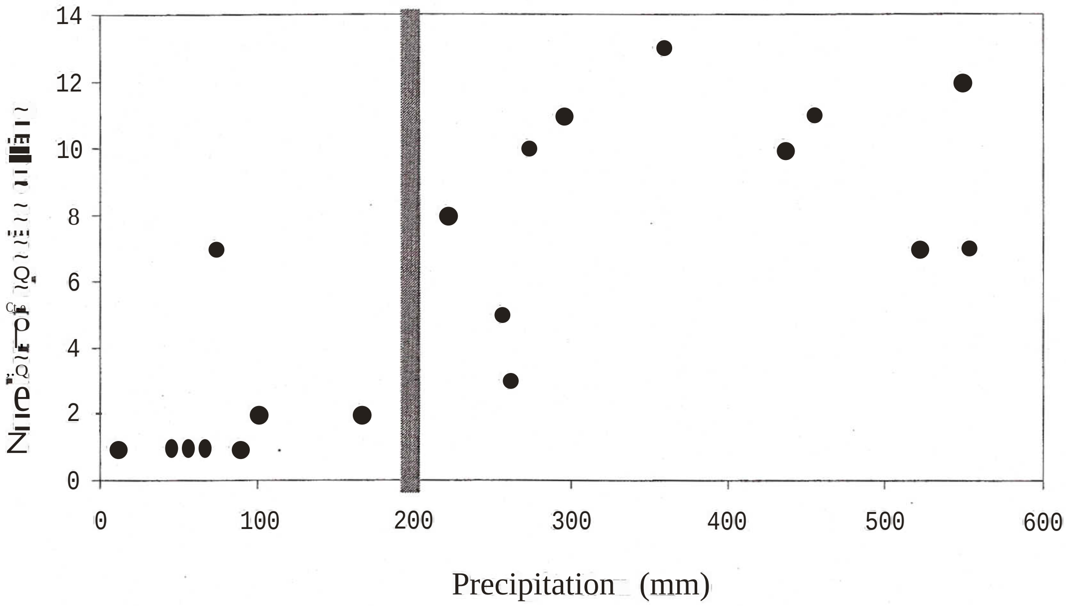


Figure 7. Activity of calling species related to precipitation. Line represents approximate threshold in activity.

The number of species that were visually observed and heard calling was strongly positively correlated with monthly precipitation totals, ($r = 0.741$, $p < 0.001$ and $r = 0.767$, $p < 0.001$ respectively) (Fig. 8). As to be expected, the number of species visually observed and calling was also strongly positively correlated ($r = 0.878$, $p < 0.001$). The number of species visually observed and the number calling rose sharply with rainfall in May, marking the start of the wet season. The number of species observed peaked in August each year, while the number calling peaked in July, with 12 in 2000 and 13 in 2001. Seven or more species called during May through September each year, then activity declined as the dry season approached.

Two months, April 2000 and June 2001, demonstrated atypical patterns in comparison to patterns observed during the rest of the study. An unusually high number of species (9) were visually observed at the Base of Hill Site during April 2000, the driest month of the study (9.6 mm precipitation). During June 2001, species activity declined sharply with the unusually low rainfall (92.5 mm), but was still greater than activity observed in dry season months with similar rainfall totals (December 2000, January and April 2001).

The highest monthly calling index and breeding acti~ity for all species regardless of site can be compared (Table 3). This table includes opportunistic sightings along the road and on trails en route to sites. The sum of species monthly calling indices can be used to represent the overall anuran calling activity for the month. The greatest sums were in July and August of 2000 and in May and July of 2001 (Table 3). Eight species (*Bufo valliceps, Agalychnis callidryas, Hyla loquax, Hyla microcephala, Hyla picta, Scinax staufferi, Smilisca baudinii*, and *Leptodactylus labialis*) were found in calling

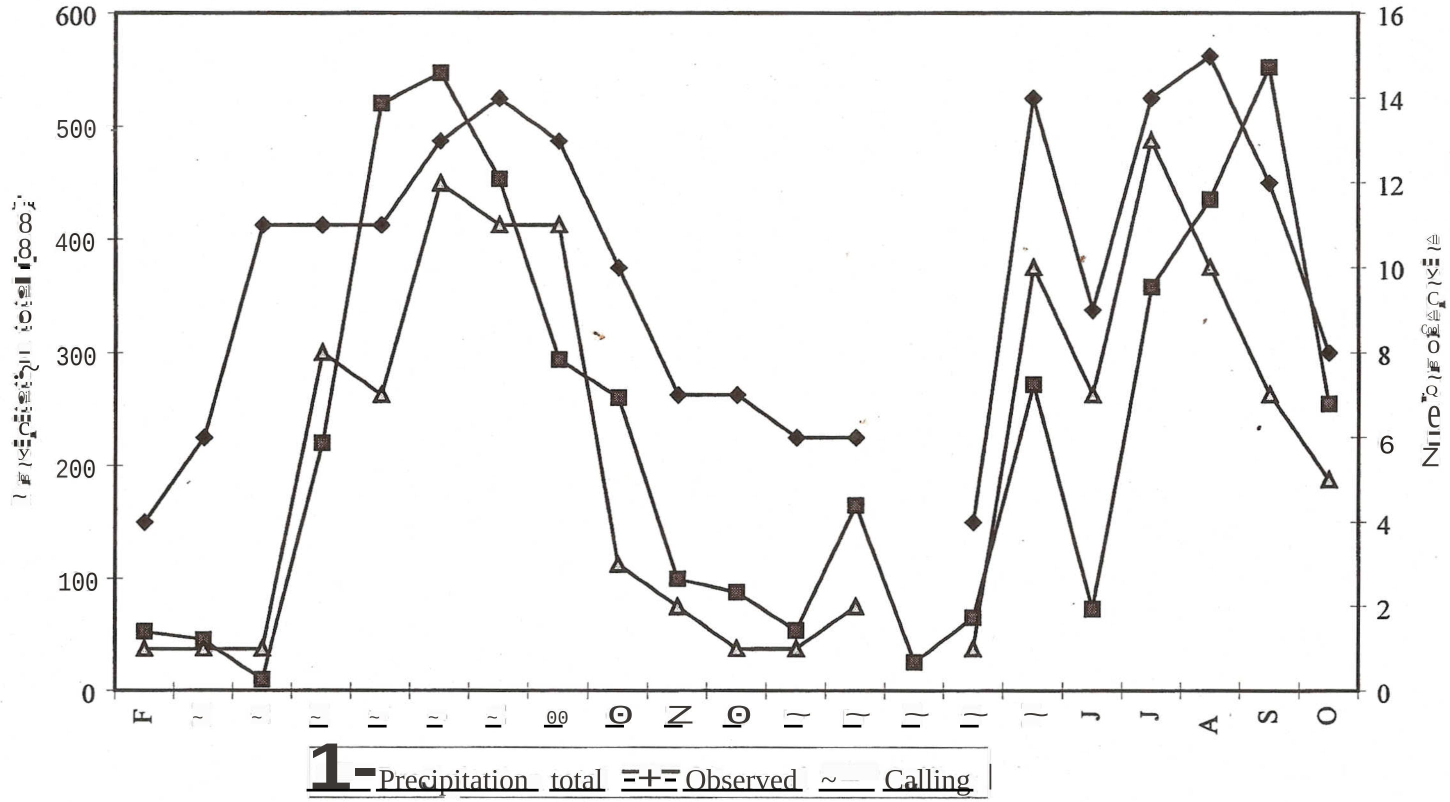


Figure 8. Number of species visually observed and calling each month with precipitation from 2000-2001 (no surveys were conducted during March 2001).

Table 3. Calling indices" and breeding activity for each species at Bladen Nature Reserve sites from 2000-2001..

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus	1	2*	1+			2	1	1+	1+	2+		2	2		2			1	1	2*	1+
Bufo valliceps			+	2+	2*+	2*+	4*+	2*+	+	+						3*+	3*+	3*+	1+	+	
Agalychnis callidryas				1	2	4*	3*	2	1	1	1					2*	2*	3*	2*	1*	1
Hyla ebraccata						2	2-	1										2			
Hyla loquax						3	2+	2	+									4*	4+	1	
Hyla microcephala				1	3	4*	3-	2	+							4*	3	4*	3	1	2
Hylapicta				2		1	3	2	1							4		4	1	1	1
Scinax staufferi				4	3	3	4	1					1			2	,1	3	1		
Smilisca baudinii				2*	2*	1	3*+	2*		+	+	+			-	4*+	4*+	3+	2*+	1+	
Smilisca cyanosticta																					
Gastrophryne elegans							+									2		'1+.	+	+	
Rana berlandieri						1*	1*+	2*+	-	+	*					2*	1*	2*		-	*
Rana vaillanti						-	+	+	+	+	+						-	-			+
Leptodactylus labialis				4	4+	2+	+	+		+		+				3	1		1	+	
Leptodactylus melanonotus					2	2	2	1							-			2	1	1-	1
Rhinophryas dorsalis				3*+	+											1+		1+	+		
Total # of species calling	1	1	1	8	7	12	11	11	3	2	1	1	2		1	10	7	13	10	7	5
Sum of calling indices	1	2	1	19	18	27	28	18	3	3	1	3	3		2	27	15	33	17	8	6

Notes: "= Highest number recorded during anyone survey each month
1 = 1-5 individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.
* = amplexus or eggs observed, + = tadpoles or metamorphs observed
- = possible breeding evidence but not confIrmed
No surveys were conducted in March 2001..

assemblages of over 50 males during the study. Of these species all except *Bufo valliceps* and *Agalychnis callidryas* were found in these large choruses during more than one month. Most species vocalized during the same months or a similar number of months each year of the study. The exceptions include *Hyla ebraccata,* which vocalized during three months in 2000 but only during one month in 2001 and *Gastrophryne elegans,* which only vocalized during 2001 for two months. G. *elegans* is an explosive breeder and may be missed unless surveys are conducted during heavy rains early in the wet season when it typically breeds.

Species differed in the season and number of months they were visually observed and breeding (Fig. 9). Seven species were visually encountered periodically throughout the entire year *(Bufo marinus, Bufo valliceps, Smilisca baudinii, Rana berlandieri, Rana vaillanti, Leptodactylus labialis,* and *Leptodactylus melanonotus),* while eight species, mostly hylids, were only encountered during the wet season, with the exception of some species in April 2000, *(Rhinophryas dorsalis, Gastrophyrne elegans, Scinax staufferi, Hyla picta, Hyla microcephala, Hyla loquax, Hyla ebraccata,* and *Agalychnis callidryas).* Monthly calling indices usually followed a pattern similar to precipitation. *H microcephala,* S. *baudinii,* S. *staufferi, L. melanonotus, R. berlandieri, A. callidryas, H picta,* and *B. valliceps* called for three or more months during the rainy season and can be characterized as continuous breeders, with evidence of breeding activity observed during four or five months (Table 4). Two species can be described as explosive breeders, *R. dorsalis* and G. *elegans;* both vocalized only after heavy rains in the beginning of the wet season. *H ebraccata* and *H loquax,* typically began reproductive activity later in the rainy season, while *L. labialis* began and ended earlier in the wet season. *B. marinus* was

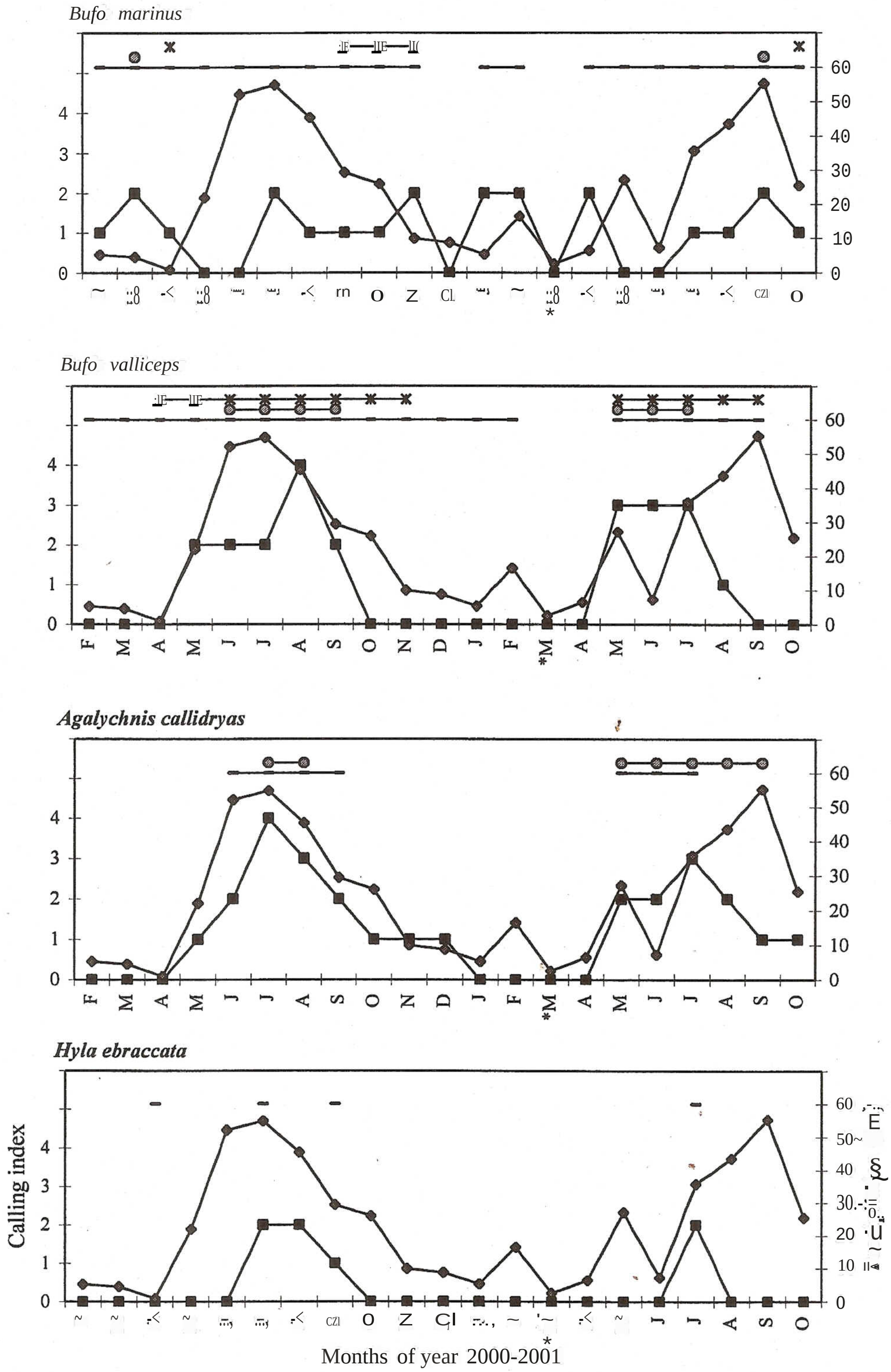
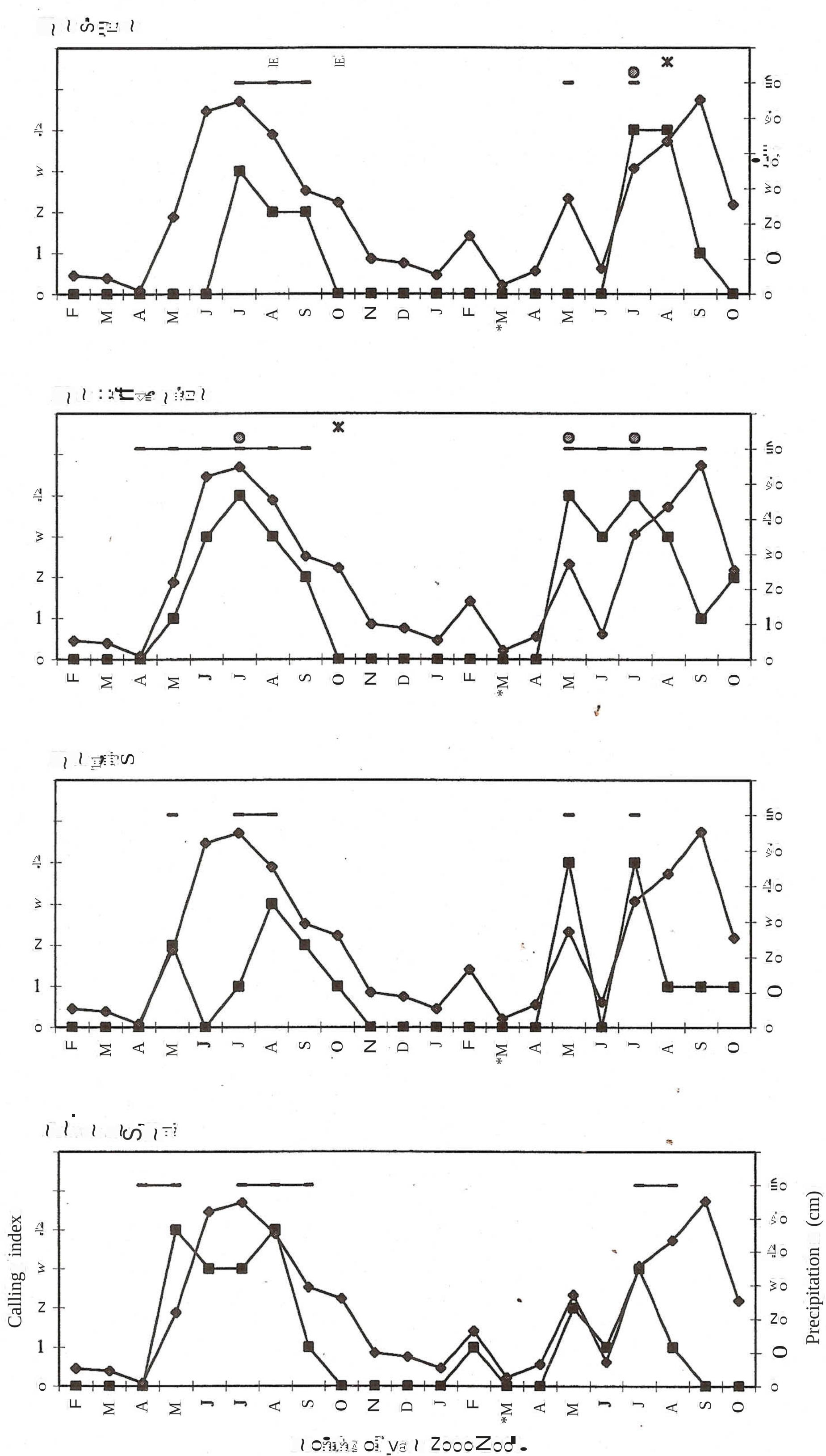


Figure 9. Calling indices and activity for each species across all BNR sites during the study. Calling index is represented by squares and precipitation is represented by diamonds. The months the species was observed is represented by a line at the top of each figure; amplexus or eggs observed are represented by circles; and tadpoles or metamorphs are represented by stars.


Calling index
Precipitation (cm)
F M A M J J A S O N D J F *M A M J J A S O

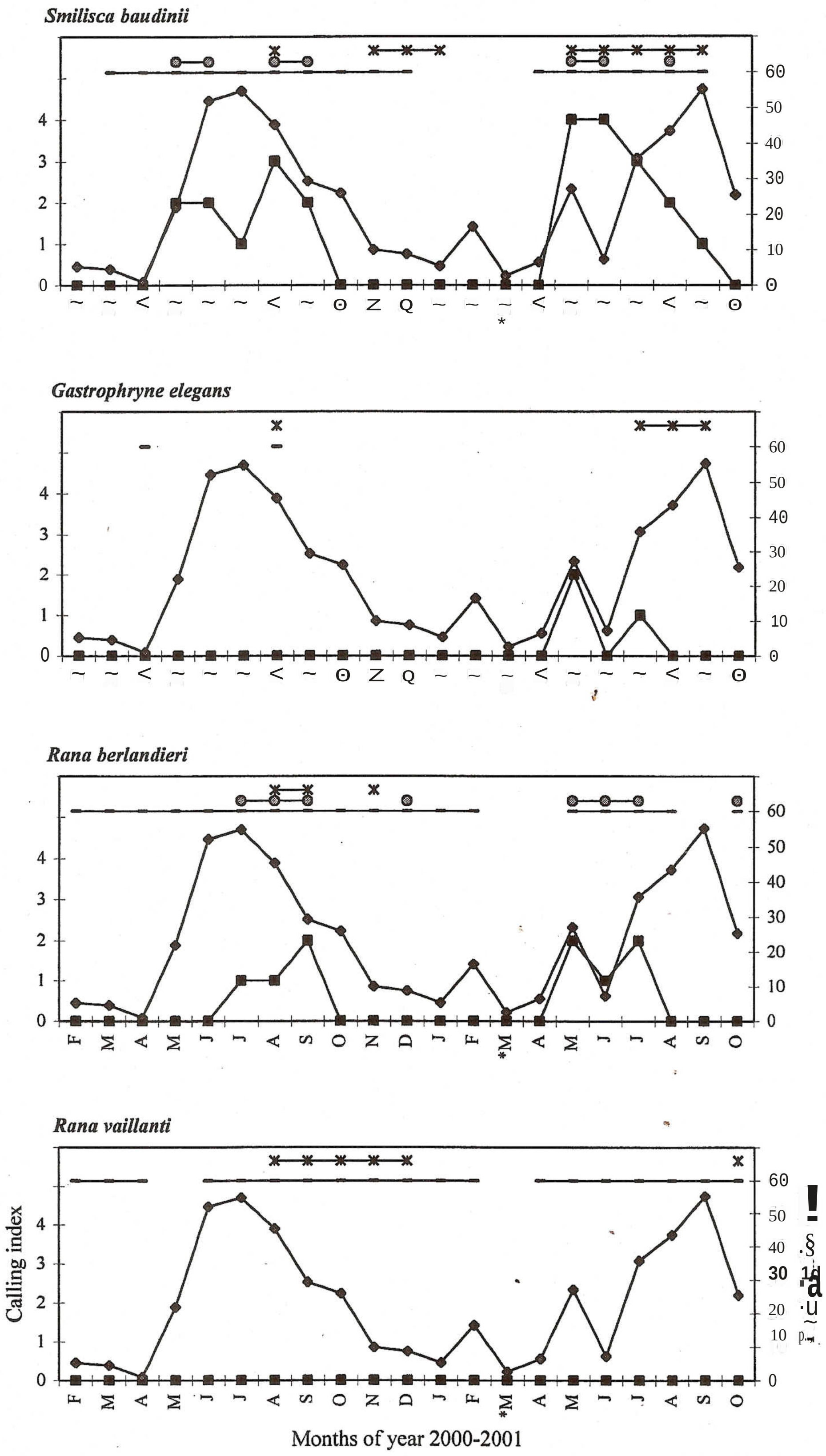


Figure 9. Continued.

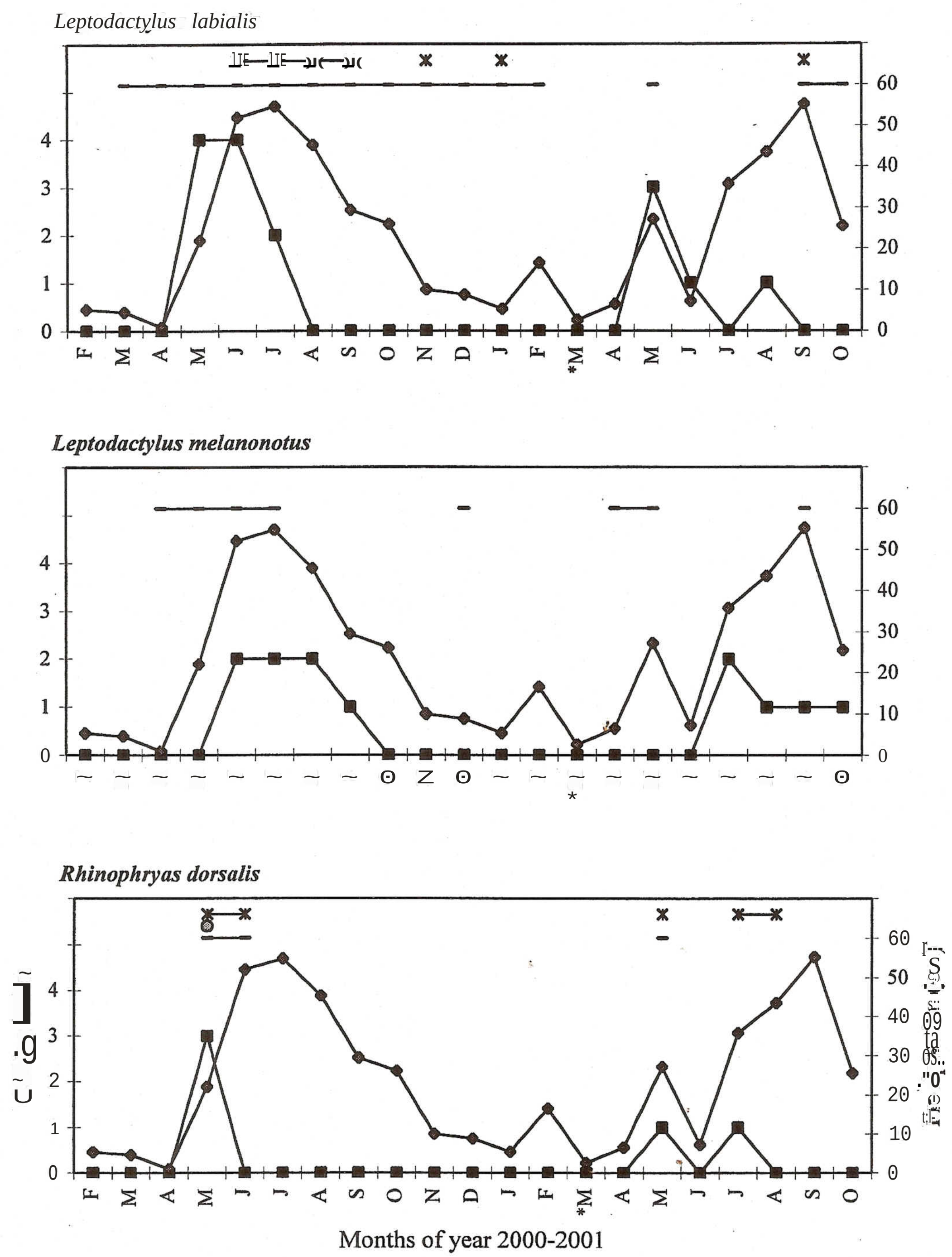


Figure 9. Continued.

Table 4. Observed duration of breeding activity across all BNR sites.

2 months	3 months	4 months	5 months
Gastrophryne elegans (1*)	*Hyla ebraccata* (1+)	*Scinax staufferi* (1)	*Smilisca baudinii* (1)
Rhinophryas dorsalis (1*)	*Leptodactylus labialis* (1*)	*Leptodactylus melanonotus* (1+)	*Hyla microcephala* (1)
	Hyla loquax (1+)	*Rana berlandieri* (1)	*Bufo valliceps* (1)
		Agalychnis callidryas (J)	*Bufo marinus* (3)
		Hyla picta (1)	

Notes: 1=rainy season only, 2=dry season only, 3.=rainy and dry seasons
* = early in rainy season, + = late onset in rainy season

the only species found to breed during both the wet and dry seasons. More details about each species reproductive activities are described in the section titled "Species Accounts" below.

Spatial Distribution of Anuran Activity

Anuran species did not utilize the study sites equally (Table 5) or microhabitat within the sites such as perch height (Fig. 10; Table 6). Furthermore, water presence influenced the number of species active at each site (Fig. 11).

The number of sites where a species was visually observed ranged from zero to eight (Table 5); *Bufo valliceps, Smilisca baudinii,* and *Rana berlandieri* were found at seven or eight sites. *Rhinophryas dorsalis* was only encountered at two sites and *Hyla ebraccata*, *Hyla picta*, *Gastrophyrne elegans, Leptodactylus labialis*, and *Hyla loquax* were found at three sites. The single visual observation of *Smilisca cyanosticta* was in the forest along the road (i.e., not at a site). The number of sites where a species vocalized ranged from zero to seven (Table 5); *Hyla microcephala* and *Scinax staufferi* called at seven sites. Patterns in species presence reflect the general abundance and level of habitat specificity of each species; with *B. valliceps, H. microcephala, S. baudinii, Leptodactylus rnelanonotus, R. berlandieri,* and *R. vaillanti* 1;>eingcommon, habitat generalists and *R. dorsalis, A. callidryas, H. loquax, H. ebraccata*, and *G. elegans* being less common, specialists of forest habitat. *H. picta, S. staufferi*, and *L. labialis* were typically observed in savanna habitat, but were also encountered and/or heard vocalizing on isolated occasions in forested sites. *B. marinus* was visually observed at all sites on the road and at the Disturbed Site, yet it was only observed breeding at the Bladen River

Table 5. Site occurrence and activity of species during study period.

	Bladen River N=67	Base of Hill n=50	Forest Entrance n=51	Forest n=42	Forest Pool n=30	Transition Pool n=31	Savanna 100m n=29	Savanna n=41	Disturbed n=6	Other locations on road n=67	# Sites observed	# Sites calling	# Sites breeding
Bufo marinus	OCB	O	O				O		OC	O	5	2	1
Bufo valliceps	OCB	OCB	OCS	O S*		OC	OCS	O	OC	OCS	8	6	4
Agalychnis callidryas		OCS	OCS	C	OCB	OCS				OCS	4	5	4
Hyla ebraccata		OC	OC		OC						3	3	0
Hyla loquax		OCB	OCB		OC						3	3	2
Hyla microcephala		OC	OCB		OCB	OC	C	C	OC	OC	5	7	2
Hylapicta		C	OC	OC		OC	C			OC	3	5	0
Scinax staufferi	C		C		C	OC	OC	OC	OC	OC	4	7	0
Smilisca baudinii	O B	OCB	OCS	OCB	O	O S	OCS		OC	OCB	8	5	6
Smilisca cyanosticta										O	0	0	0
Gastrophryne elegans		O	O	O S*	B	C				OC	3	1	1
Rana berlandieri	O S	OCB	OCB			O	OCS	OCS	O	OCB	7	4	5
Rana vaillanti	O	O B	OCB		O	O	O S			O S	6"	0	0
Leptodactylus labialis		OC					OCB	OCS		OCS	3	3	2
Leptodactylus melanonotus		O	OC		OC	OC	C		C	OC	4	4	0
Rhinophryas dorsalis		OC	OCB		B					QC	2	2	2
Total Species Richness	6	14	14	5	10	10	10	5	7	14			

Notes: 0 = observed, C = calling, B = breeding confirmed by observation of amplexus or presence of eggs, tadpoles, or metamorphs.
* = only evidence of breeding was immature individuals, successful breeding within the site was never confirmed
n = number of field days in the site
Last three columns include only the 9 sites (do not include other locations on road)

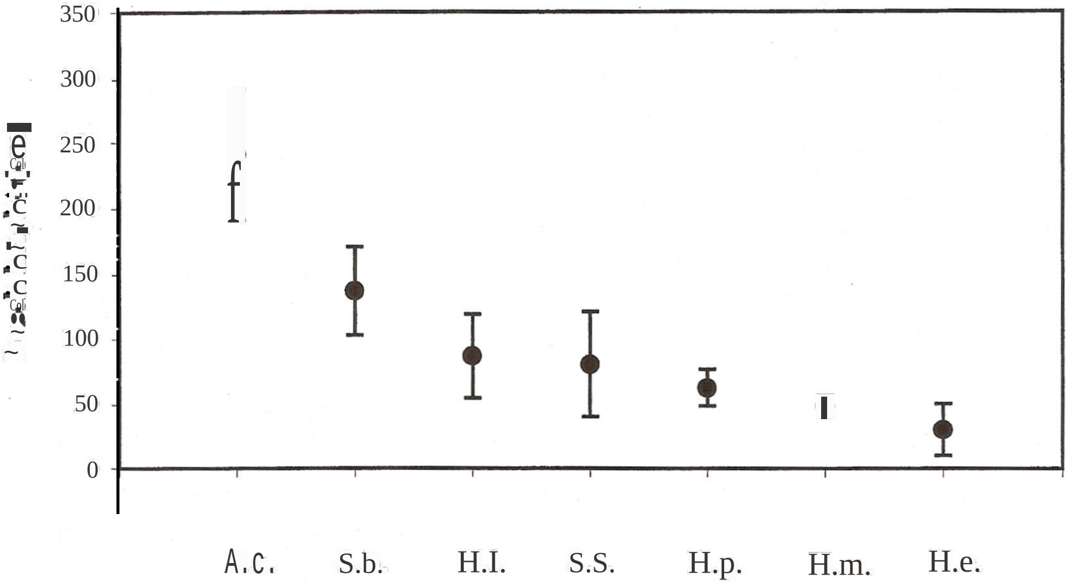


Figure 10. Mean perch heights with 95% confidence intervals for species of Hylidae encountered during study.

Table 6. Mean perch heights for species of Hylidae.

Species	Mean perch height (cm)	n
A. callidryas	241 [a]	44
S. baudinii	136 [b]	32
H loquax	86 [bc]	13
H microcephala	48 [c]	80

Different superscript letters indicate significant differences at $p < 0.05$ with Tamhanes test.

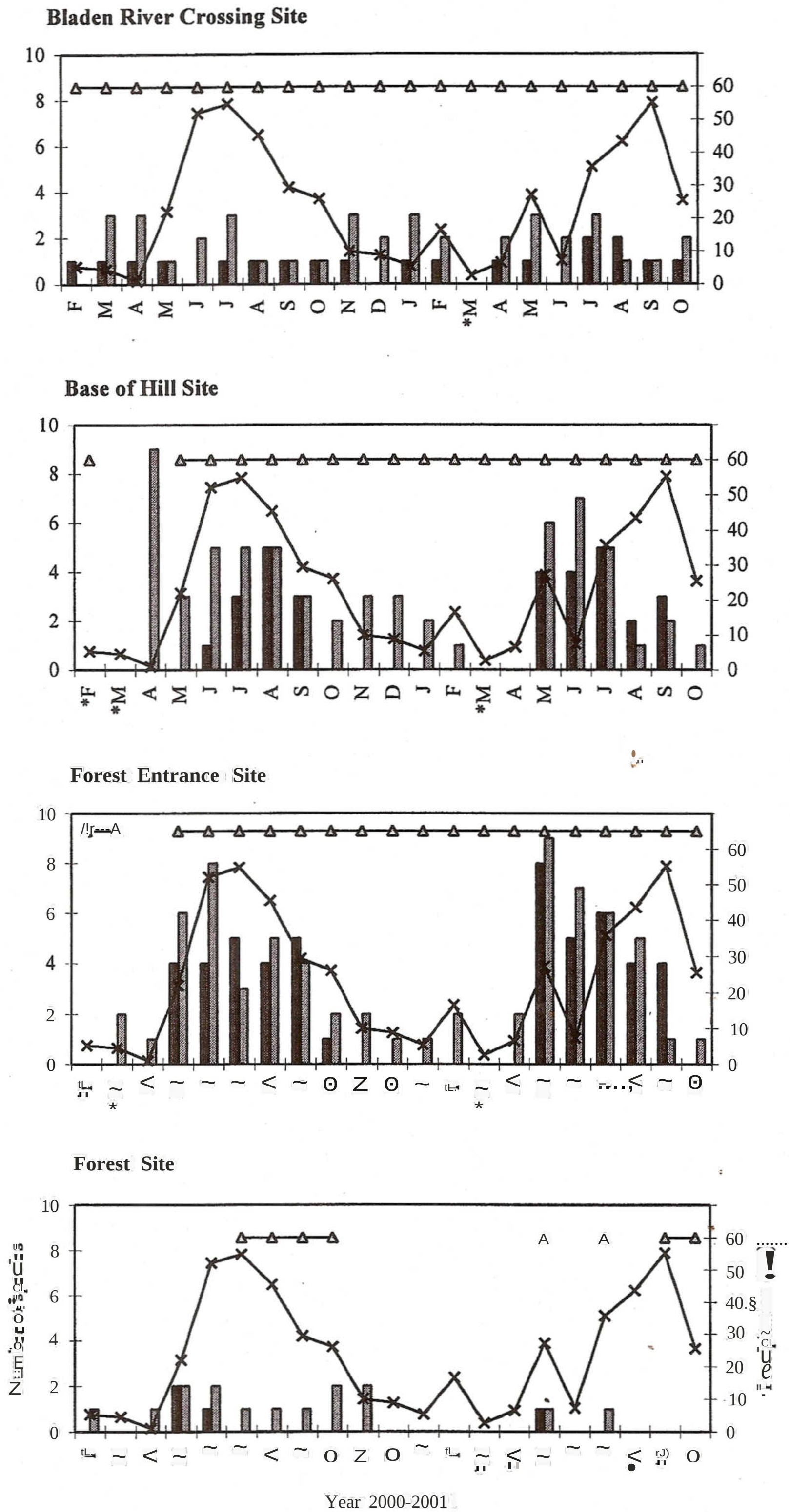


Figure 11. The number of species active at each site per month of study. Light bars indicate visually observed species, dark bars indicate calling species, triangles indicate months with standing water present in the site, and asterisks next to months indicate when surveys were not conducted at the site.

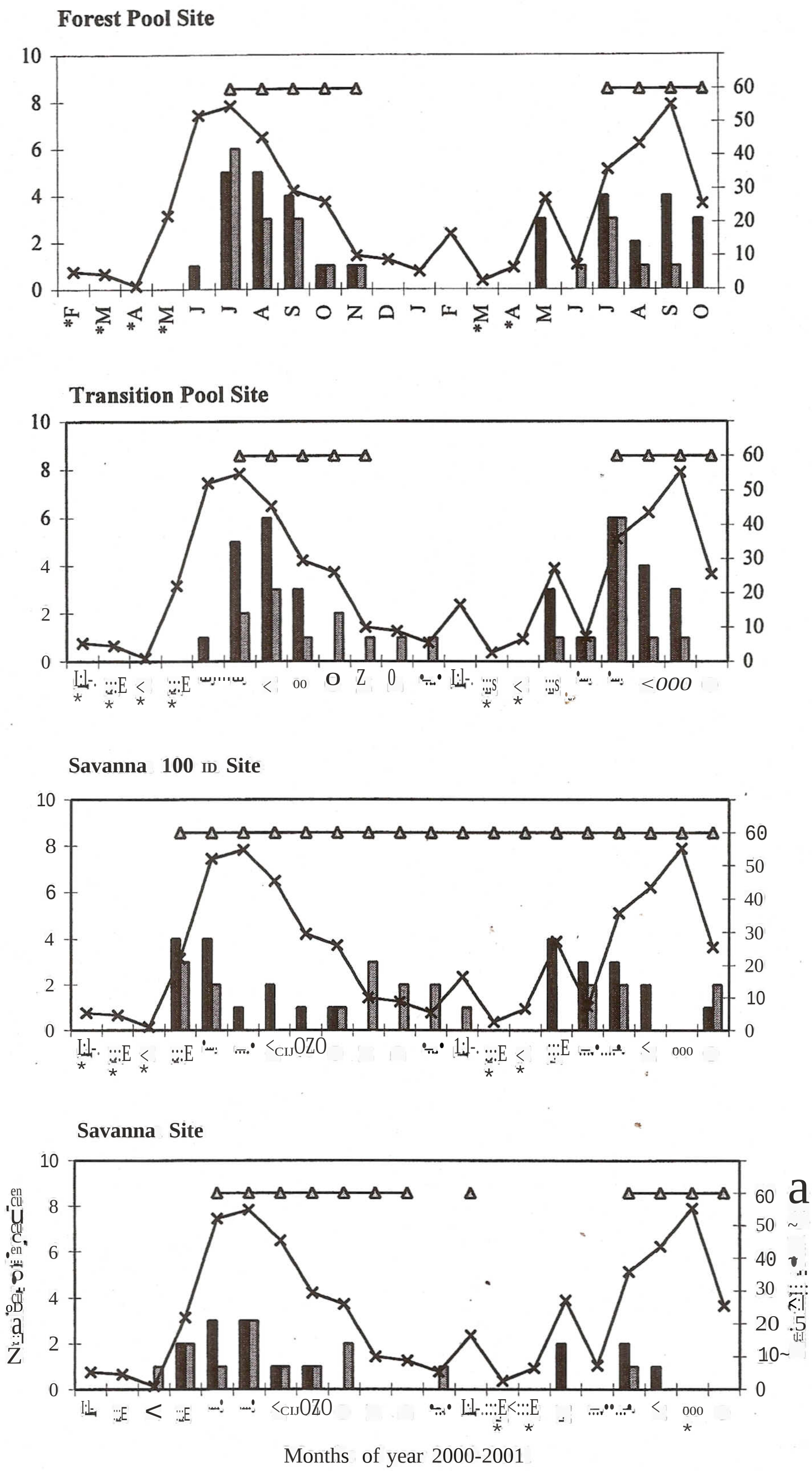


Figure 11. Continued.

Crossing Site.

Habitat was partitioned in a vertical manner within each site by species use of different perch heights (Fig. 10). The confidence intervals overlap for species perching at heights less than 100 cm. The mean perch heights of species with a sample size greater than 10 were found to be significantly different ($F^{t}_{,3}$ = 34.51, $p < 0.0001$) (Table 6). *Agalychnis callidryas* perched higher than all other hylid species ($p < 0.05$). *Hyla microcephala* perched at lower heights, significantly different from *Smilisca baudinii* and *A. callidryas* ($p < 0.05$) but not from *Hyla loquax*.

Water presence was related to the number of species active in each site throughout the study (Fig. 11) as it strongly influenced breeding in some species. The number of species observed or calling per month during the wet season followed a normal distribution, oftentimes skewed to the right especially at temporary pool sites. This illustrated the trend of increasing activity with the start of the rains, with the highest number of species active a month or two after the rains began and then a gradual decline in activity as the wet season progressed and ended. Four sites had semi-permanent or permanent pools (Bladen River Crossing Site, Base of Hill Site, Forest Entrance Site, and Savanna 100 m Site) and a great number of species active early in the wet season, except for the Bladen River Crossing Site. The remaining four sites (Forest Site, Savanna Site, Forest Pool Site and Transition Pool Site) had temporary pools that filled with water by June or July, after one or two months of heavy rains. However, species were visually observed or calling at these sites in May and June, regardless of the lack of standing water (Fig. 11). Usually activity was greatest in July at these sites, declining each month thereafter.

Additional tables, including the highest calling index and number of individuals, in addition to breeding activity of species observed at each site each month can be found in Appendices 1 – 9. Details describing species activity at each site are described in the section titled "Site Activity" below.

Vegetation Characteristics

Descriptive statistics for vegetation characteristics varied among the seven sites (Table 7) and helped to explain differences in species richness and composition. Mean canopy cover was over 80% at the Forest site and Forest pool site, while the Disturbed Site and Savanna 100 m Site had less than 10% canopy cover. Mean vegetation height was highest at the Savanna Site (89.71 cm) and lowest at the Forest Site (0.77 cm). Vegetation structure measurements and total DBH of trees mirrored patterns of canopy cover and vegetation height found at sites (Table 7). Mean canopy cover and medium and high vegetation structure had a strong positive correlation ($r = 0.929$, $p = 0.002$) as did vegetation height and low vegetation structure ($r = 0.921$, $p = 0.003$) (Table 8). Strong positive correlations were also present between medium and high vegetation structure ($r = 0.901$, $p = 0.006$) and between total DBH of trees >10 cm and high vegetation structure ($r = 0.744$, p= 0:055) and number of trees >10 cm **DBH** ($r = 0.938$, $p = 0.002$). Therefore, additional analyses to compare vegetation characteristics at sites were confined to two uncorrelated variables, canopy cover and vegetation height.

Mean canopy cover was found to be significantly different between sites (Chi-square = 373.96, df = 6, $p < 0.0001$) (Kruskal-Wallis non-parametric test) (Table 7). The Forest Site and Forest Pool Site were not significantly different from each other, but were significantly different from the other sites. In addition, the Forest Entrance Site and Base

Table 7. Descriptive statistics for vegetation characteristics at seven sites.

Site Name	Mean canopy cover (%)	SE	Mean vegetation Height (cm)	SE	Vegetation structure 0-2.5 m	SE	Vegetation structure 2.5-5 m	SE	Vegetation structure 5-30 m	SE	Number of trees DBH>lOcm	Total DBHof trees> 10cm
Forest Site	83.71'	1.11	0.77'	0.41	0.00	0.00	0.12	0.04	0.76	0.06	6	181.21
Forest Pool Site	82.95'	1.61	1.65'	0.74	0.26	0.06	0.18	0.05	1.27	0.07'	8	229.14
Forest Entrance Site	61.74^{b}	2.64	15.26^{b}	2.10	0.06	0.03	0.06	0.03	0.59	0.06	1	11.46
Base of Hill Site	57.58^{b}	3.42	68.55^{cdO}	7.36	0.45	0.05	0.15	0.00	0.50	0.03	1	21.65
Savanna Site	18.18°	1.46	89.71^{cc}	4.07	0.85	0.09	0.00	0.00	0.00	0.00	3	67.52
Savanna 100 m Site	8.52°	1.46	52.58^{cd}	5.14	0.45	0.08	0.02	0.02	0.00	0.00	5	59.88
Disturbed Site	O.OOd	0.00	5.85^{r}	0.57	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00

Different superscript letters indicate significant differences at $p < 0.05$ with Tamltanes test.

Table 8. Pearson correlation coefficients for seven vegetation variables at seven sites (excluding Transition Pools Site and Bladen River Crossing Site). Lower number in each pair is the p-value.

	Mean canopy cover	Mean vegetation height	Vegetation structure 0-2.5 m	Vegetation structure 2.5-5 m	Vegetation Structure 5-30 m	# trees> 10 cm DBH	Total DBH trees> 10cm
Mean canopy cover	1						
Mean vegetation height	-0.429	1					
	0.337						
Vegetation structure 0-2.5 m	-0.333	0.921	1				
	0.466	0.003					
Vegetation structure 2.5-5 m	0.879	-0.315	-0.214	1			
	0.009	0.492	0.645				
Vegetation structure 5-30 m	0.929	-0.555	-0.367	0.901	1		
	0.002	0.196	0.419	0.006			
Number of trees >10cm DBH	0.49	-0.26	0.052	0.489	0.59	1	
	0.264	0.573	0.912	0.265	0.163		
Total DBH trees >10cm	0.657	-0.398	-0.087	0.627	0.744	0.938	1
	0.109	0.376	0.853	0.132	0.055	0.002	

of Hill Site were not different from each other, but were different from the other sites, as were the Savanna Site and Savanna 100 m Site. The Disturbed Site was significantly different from all other sites. Mean vegetation height was also significantly different between sites (Chi-square = 287.97, df = 6, $p < 0.0001$) (Table 7). Sites that were significantly different from all others include the Forest Entrance Site and Disturbed Site. Similar to results for canopy cover, the Forest Site and Forest Pool Site were not different from each other but were different from the other sites.

Among the sites studied, species richness was highest at intermediate levels of canopy cover (Fig. 12) and vegetation height (Fig. 13), which were values of vegetation variables typical of sites on the road (Base of Hill Site, Forest Entrance Site, and Savanna 100 m Site). Sites off the road had either very high percent canopy cover and low vegetation height (Forest Site and Forest Pool Site) or low percent canopy cover and high vegetation height (Savanna Site). The Disturbed Site had low percent canopy cover and low vegetation height.

Species Habitat Preferences

The niche of each anuran species could be viewed as a function of its preferred habitat in regard to mean canopy cover and vegetation height at the sites where it was present during at least one month of the study (Fig. 14). Niche space, defined by these habitat variables and their respective standard errors, gives insight to species habitat preferences and community structure. Each site could 3J.sobe characterized by these variables in the same manner to compare species niche space to vegetation variables at the actual sites studied (Fig. 14). As a result of the method used in the calculation, species commonly encountered in the same sites had overlapping niche spaces. The more

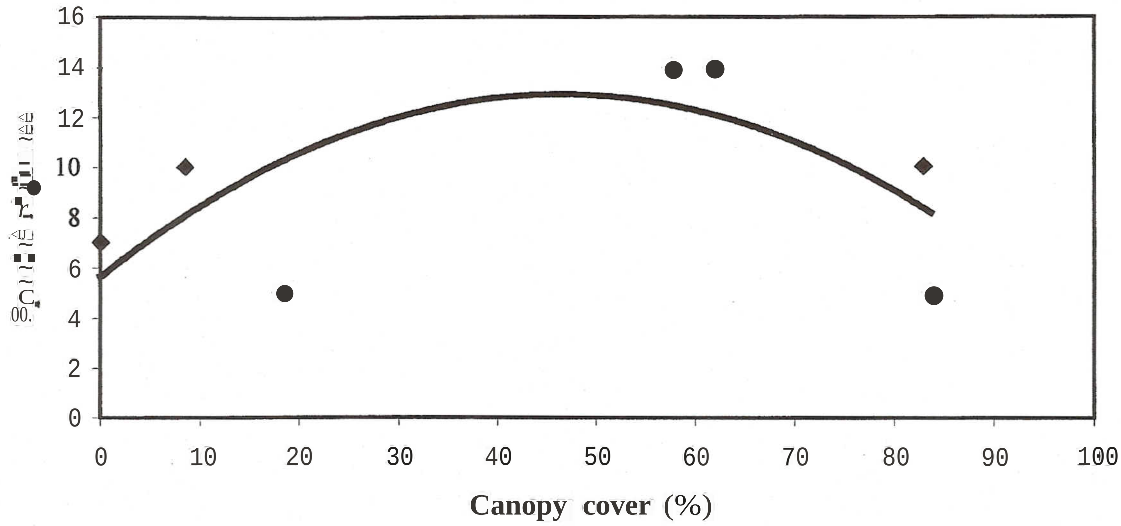


Figure 12. Species richness at sites with different canoPI cover. Nonlinear regression equation $y = -0.0034x^2 + 0.3139x + 5.6378$, $R = 0.4104$.

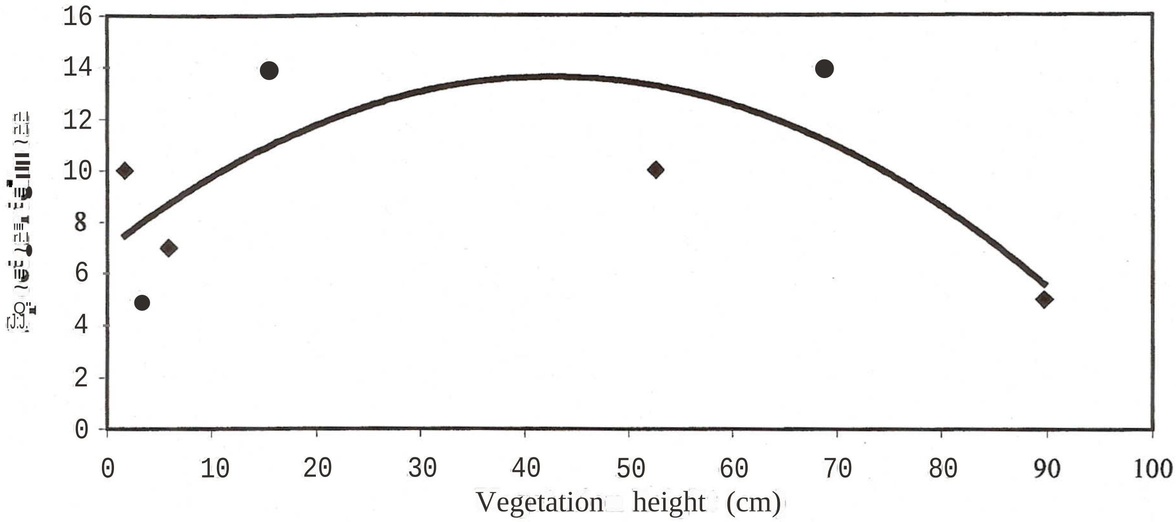


Figure 13. Species richness at sites with different vegetation height. Nonlinear regression equation $y = -0.0036\ x^2 + 0.311x = 6.9825$, $R^2 = 0.4722$.

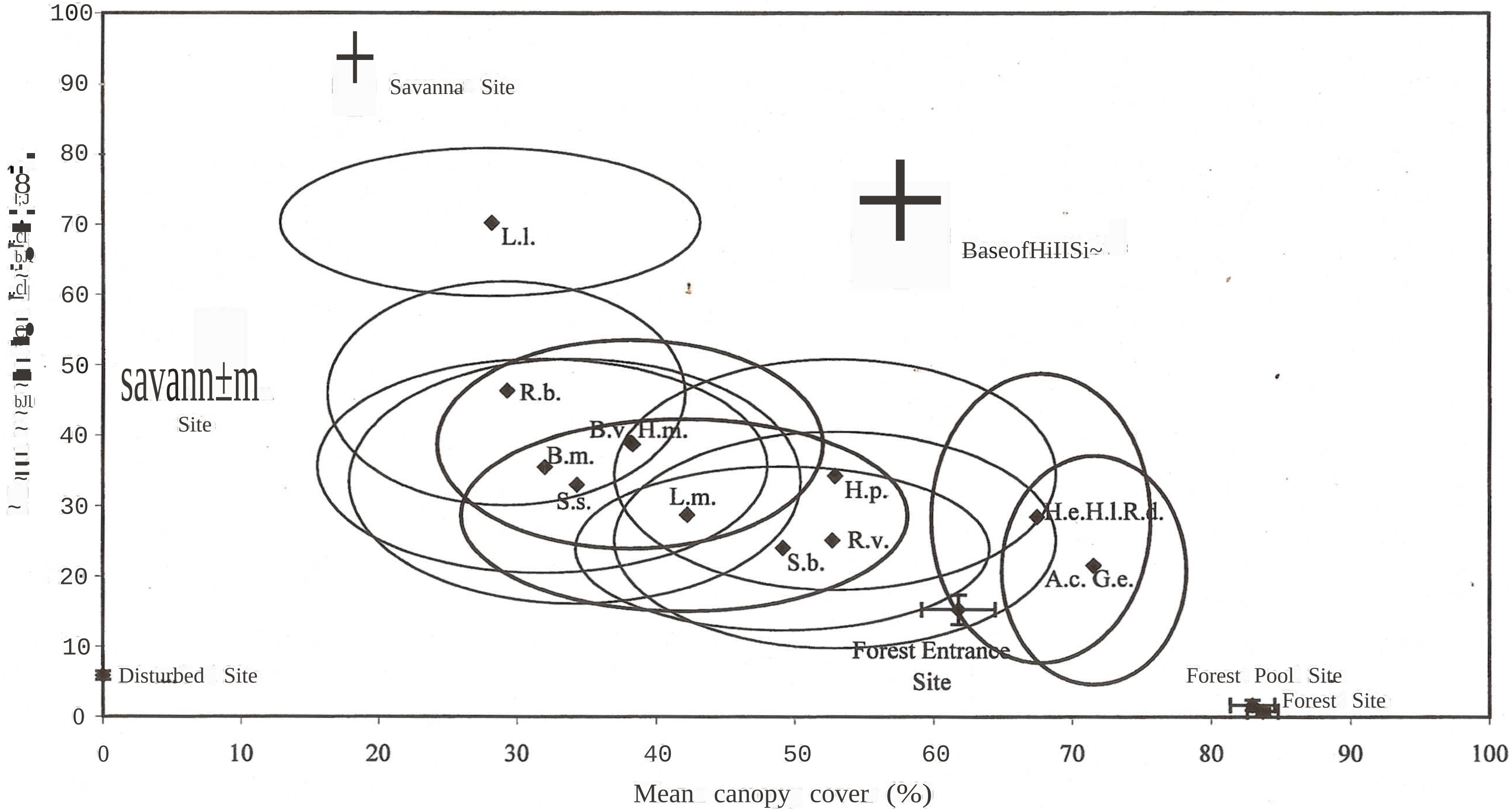


Figure 14. Representation of niche space for each species defined by mean canopy cover and vegetation height. Sites were included in the calculation of means if the species was present during at least one survey. Circles indicate +/- SE. Site means (+/- SE) are included for comparison to niche spaces.

distant the species spaces were, the more unlikely that they occurred in similar sites. Three groups could be recognized based on the proximity of their niche spaces. *Gastrophryne elegans*, *Hyla ebraccata*, *Hyla loquax*, *Agalychnis callidryas*, and *Rhinophryas dorsalis* were similar in that they are all found in sites with a closed canopy and low vegetation height (forest sites) (Fig. 14). In contrast, *Leptodactylus labialis* was typically found in sites with an open canopy and high vegetation height (Savanna Site or Savanna 100 m Site). The remaining species were found at intermediate levels of both canopy cover and vegetation height.

An estimation of preferred breeding habitat for each species could be viewed in a similar manner by limiting the calculation to only include sites where definite evidence of breeding was found during more than one month (Fig. 15). This helped to eliminate some of the noise found during 20 survey months, such as a single visual or calling observation of a species within a site. These atypical observations were usually made during the start of the wet season and although they may indicate important habitat range tolerances of the species, they probably do not represent their typical breeding habitat. Two species *(Rana vaillanti* and *Bufo marinus)* were not included in this figure because they were not found breeding in any of the sites for which habitat data was collected. *Hyla picta* and *Gastrophryne elegans* were displayed by a single point because breeding evidence for more than one month was only found within one site. *Hyla picta, Scinax staufferi*, and *Leptodactylus labialis* could be regarded as breeding specialists of sites with an open canopy and high vegetation height (savanna sites), whereas *Hyla loquax, Agalychnis callidryas, Hyla ebraccata, Gastrophryne elegans*, and *Rhinophryas dorsalis* specialized in sites with a more closed canopy and low vegetation height (forest sites).

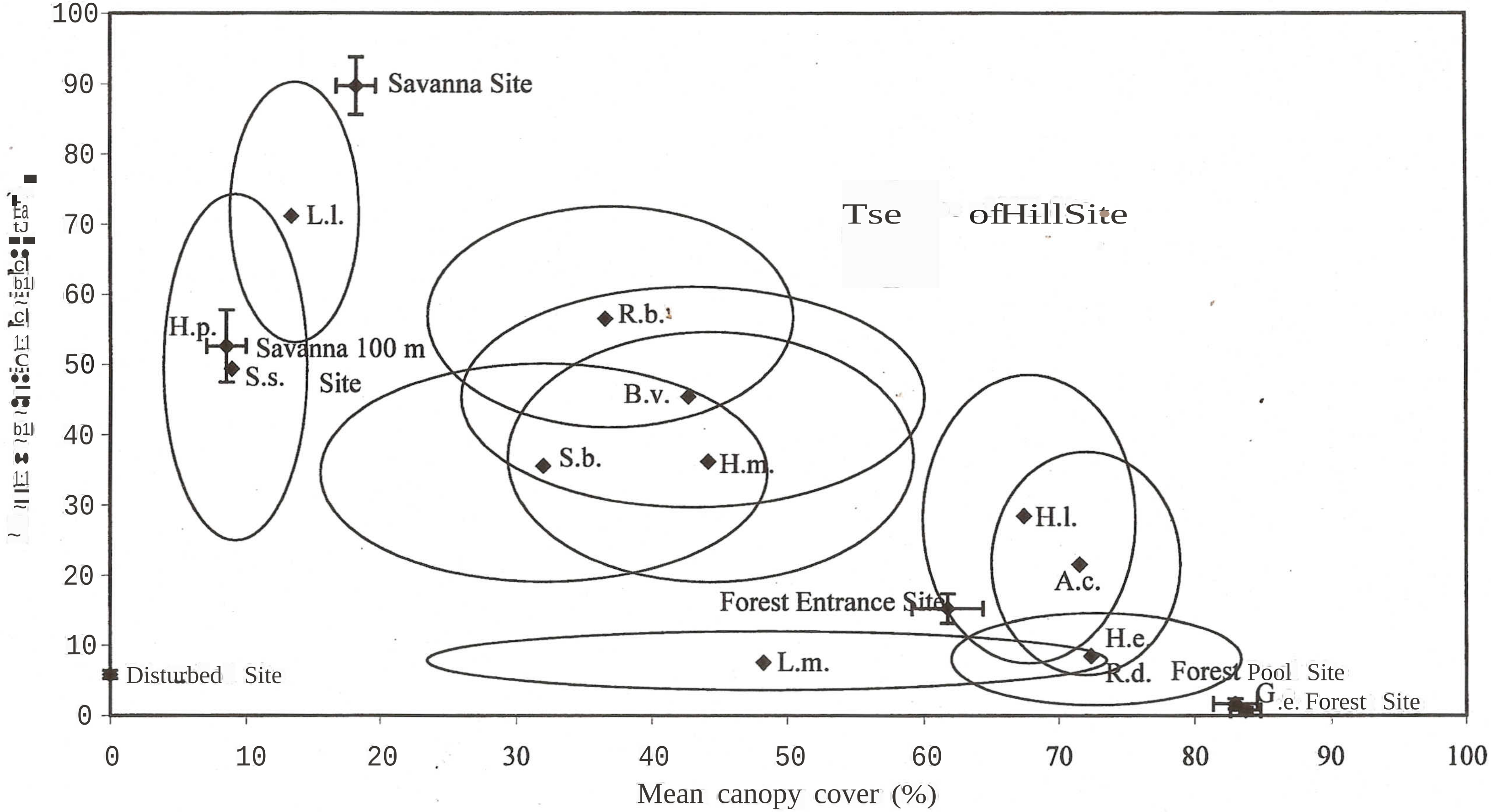


Figure 15. Representation of niche space defined by mean canopy cover and vegetation height for each species. A site was included in the calculation only if more than one observation of breeding activity for the species occured within the site. Circles indicate +1- SE. Site means (+1- SE) are included for comparison to niche spaces.

However, *H. picta* and *S. staufferi* were also commonly encountered calling at the Transition Pool Site, which was not included in this analysis because habitat variables were not available. *Leptodactylus melanonotus* specialized in sites with low vegetation height and varying canopy cover. The remaining species (*Rana berlandieri, Bufo valliceps, Hyla microcephala,* and *Smilisca baudinii*) have a broad niche space with high variation in canopy cover and vegetation height and can be regarded as habitat generalists.

Jaccard similarity values demonstrate further evidence in support of species preference of certain habitat. Sites with a high number of identical species had coefficient of Jaccard similarity values close to a value of 1.0 (Table 9). The Forest Entrance Site and Base of Hill Site had a high Jaccard value (0.87), reflecting their proximity in location and hence similar vegetation characteristics such as canopy cover and the same surrounding broadleaf forest. All of the species observed at the Forest Pool Site (10) and Transition Pool Site (10) sites also occurred in the Forest Entrance Site (14), Jaccard values of 0.71, yet the Forest Pool Site and Transition Pool Site were not very similar in species composition (0.54). The Transition Pool Site did not have some of the specialist species encountered in the Forest Pool Site and vice versa. The Savanna Site and Forest Site had a very low Jaccard value (0.11), demonstrating the difference in species presence at sites with contrary values of canopy cover and vegetation types (Table 7 & 9). The Forest Site was also notably different in species composition to the Disturbed Site (0.20) and the Forest Pool Site was different from the Savanna Site (0.15). Overall, sites with similar habitat characteristics had similar species present.

Table 9. Similarity of species presence at all nine sites. Numbers in parentheses are species richness at each site, italicized numbers are the Jaccard coefficient of similarity values, and numbers in regular type are the number of species in common between the two sites.

	Bladen River (6)	Base of Hill (14)	Forest Entrance (14)	Forest (5)	Forest Pool (10)	Transition Pool (10)	Savanna 100 m (10)	Savanna (5)	Disturbed (7)
Bladen River (6)	---	5	6	2	3	5	6	3	5
Base of Hill (14)	*0.33*	---	13	5	9	9	9	4	6
Forest Entrance (14)	*0.43*	*0.87*	---	5	10	10	9	4	7
Forest (5)	*0.22*	*0.36*	*0.36*	---	3	3	3	1	2
Forest Pool (10)	*0.23*	*0.60*	*0.71*	*0.25*	---	7	5	2	4
Transition Pool (10)	*0.45*	*0.60*	*0.71*	*0.25*	*0.54*	---	8	4	6
Savanna 100 m (10)	*0.60*	*0.60*	*0.60*	*0.25*	*0.33*	*0.67*	---	~	7
Savanna (5)	*0.38*	*0.27*	*0.27*	*0.11*	*0.15*	*0.36*	*0.50*	---	4
Disturbed (7)	*0.63*	*0.40*	*0.50*	*0.20*	*0.31*	*0.55*	*0.70*	*0.50*	---

Site Activity

Anuran activity at each site was dynamic, characterized by variable change in species composition and abundance during each month, season, and year of the study. Site attributes, such as water permanency, as well as anuran behavior and habitat preferences influenced the patterns observed. Trends in anuran activity will be discussed for each site with reference to the number of species observed, calling, and breeding.

Bladen River Crossing Site

Flowing water persisted year round at the Bladen River Crossing Site and a total of six species were observed during the study (Fig. 11; Table 5). Observations included activity at a pool in the floodplain on the south side of the river. Activity occurred year-round, with at least one species visually observed or calling each month. The number of species encountered varied between zero and three each month, while the number calling was between zero and two (Appendix 1).

Four species (*Bufo marinus, Bufo valliceps, Rana berlandieri*, and *Rana vaillanti*) were regularly encountered at the Bladen River Crossing Site during the study. *B. marinus* was the only species observed to breed in the river itself. It called at index 1 or 2 periodically during the wet and dry seasons at slow sections of the river. *B. valliceps* called at a floodplain pool during May, July and August 2001 and eggs were observed in July. *R. berlandieri* called and deposited egg masses at the same pool in October 2001.

Observations of two more species were made during the study. A *Smilisca baudinii* adult and numerous tadpoles were observed in a floodplain pool during December 2000 and January 2001. *Scinax staufferi* called only during one month, May

2000, and no visual observations were made, so it is unlikely that it commonly uses this site.

Base of Hill Site

Pools at the Base of Hill Site were semi-permanent, drying during two months (March and April 2000) of the study (Fig. 11). Total species richness of the site was 14 and six species were observed breeding (Table 5). The number of species encountered monthly varied between zero and nine, while the number of species vocalizing was between zero and five (Appendix 2).

At least one species was encountered at the Base of Hill Site each month of the study excluding April 2001. Three species, *Gastrophryne elegans*, *Hyla ebraccata*, and *Leptodactylus labialis,* were only encountered at the site during April 2000, the driest month of the study (9.6 mm total precipitation) when the pools were dry. Six more species were encountered during this dry month, yet no activity was observed during the following April 2001. *Leptodactylus melanonotus* was encountered during April and December 2000, and *Rhinophryas dorsalis* and *Hyla loquax* were only encountered during 2001. The remaining seven species were visually observed during both years of the study.

Vocalizing species were observed from June to September in 2000 and May to September in 2001. More species called earlier in the wet season in 2001 compared to 2000; nine species called during May to July in 2001 while only three species called during the same time period in 2000. *Agalychnis callidryas* and *Hyla loquax* called for an equitable number of months each year. *Bufo valliceps* called only during August 2000 at index 4 and five species (*Hyla picta, Rana berlandieri, Hyla ebraccata, Rhinophryas* *doraslis,* and *Leptodaetylus labialis)* called only during one month in 2001 at indices 1 or 2. Breeding activity was reported for five species in 2001 and four species in 2000.

Forest Entrance Site

Pools at the Forest Entrance Site were filled during every month ofthe study except April 2000 (Fig. 11). Total species richness at the site was 14 and evidence of breeding activity was reported for eight species (Table 5). The number of species visually observed per month ranged from zero to nine and the number of species calling ranged from zero to eight (Appendix 3).

Species were visually observed within the site during every survey month. The number of species encountered noticeably increased at the beginning of the rainy season then declined until reaching a low of one or two species per month during the dry season. Two species were only observed during one month ofthe study, 17 individuals of *Gastrophryne elegans* were found on one survey in April 2000 and one *Hyla pieta* individual was encountered during May 2001. The other 12 species were encountered during both years of the study.

Calling began immediately with the start of the rainy season in May, with four species calling in 2000 and eight calling in 2001. Three species *(Bufo valliceps, Hyla pie ta,* and *Scinax staufferi)* called only during 2001, while 10 species called during both years. Higher calling indices and more breeding observations were recorded during more months in 2001 compared to 2000, particularly for *B. vallieeps, Hyla microeephala, Smilisea baudinii,* and *Rana berlandieri.* Tadpoles, assumed to be that of *Leptodaetylus melanonotus,* were reported in the pools as early as April in 2001.

Forest Site

The Forest Site temporary pool filled with water during several surveys in the rainy season; however, it always drained within a few hours to a couple days after filling (Fig. 11). Therefore, activity at this site was never great and only five species were encountered during the study (Table 5). The number of species encountered and calling ranged from zero to two during each month (Appendix 4). Breeding evidence was reported for three species, in the form of immature individuals of *Bufo valliceps* and *Gastrophryne elegans* and eggs of *Smilisca baudinii*.

Bufo valliceps and *Smilisca baudinii* were the only two species regularly encountered at the Forest Site. *B. valliceps* was visually observed during the wet and dry seasons, while S. *baudinii* was only observed during the wet season. Two species were only encountered during one month in 2000, *Hyla picta* during May and *Gastrophryne elegans* during August.

Calling individuals of three species (*Agalychnis callidryas*, *Hyla picta*, and *Smilisca baudinii*) were observed at the Forest Site, the first species during May and June 2000 and the latter two species during one month each, May 2000 and May 2001 respectively. Unidentified tadpoles were observed in the pool on a couple different occasions; however, it was likely that they were washed into the pool from other areas since successful reproduction was never observed in the site. Breeding attempts were occasionally made, for instance, after one night of heavy rain early in the wet season (28 May 2001, 9:00 h), a *Smilisca baudinii* chorus was observed in the pool. Eggs were deposited but the pool was dry the next day by 13:00 h.

Forest Pool Site

The Forest Pool Site had a temporary pool that filled with water by July each year. The pool remained filled until after November surveys in 2000 and beyond the end of the study in 2001 (Fig. 11). Total species richness at this site was 10 and breeding observations were reported for four species (Table 5). The number of species encountered per month varied between zero and six, while the number that called was between zero and five (Appendix 5).

Species were visually observed within the Forest Pool Site from July to November 2000 and June to September 2001. Three species, *Agalychnis callidrays, Hyla microcephala,* and *Rana vaillanti*, were encountered during both years of the study. *Hyla ebraccata, Hyla loquax, and Leptodactylus melanonotus* were only encountered during July 2000, but each vocalized during both years. One individual of *Smilisca baudinii* was visually observed during June 2001..

Observations of calling individuals began during Mayor June, a month or two before the pool filled with water. For *example"Leptodactylus melanonotus* called during June 2000 and three species including *Agalychnis callidryas, Hyla microcephala,* and *Scinax staufferi* called at index 1 in May 2001.. No calling was heard during June 2001, when rainfall was only 47.5 mm, uncharacteristically low for this month, but in July calling resumed and the pool filled with water. Five species called during both years but S. *staufferi* only called during May 2001.. Calling peaked in July each year, then declined in intensity and the number of species until the dry season. Egg masses of *A. callidryas* were reported each year but observations of amplexing *H microcephala* individuals were only reported during July 2001.. Tadpoles of two species were only reported during 2001, that of *Gastrophryne elegans* from July to September and of *Rhinophryas dorsalis* during July and August..

Transition Pool Site

The temporary pool at the Transition Pool Site was present from July to October 2000 and from July until the end of the study in 2001 (Fig. 11). Total species richness of the site was 10, but evidence of breeding was observed for only two species *(Agalyehnis eallidryas* and *Smilisea baudinii)* (Table 5). The number of species encountered and calling ranged from zero to six each month (Appendix 6).

Species were visually observed in the site from July 2000 to January 2001 and from May to September 2001. Five species were encountered during both years of the study *(Bufo vallieeps, Hyla mieroeephala, Hyla pieta, Rana berlandieri,* and *Rana vaillanti).* Three species were encountered during only one survey month, *Scinax staufferi* in July 2000, *Agalyehnis eallidryas* in July 2001, and *Leptodaetylus melanonotus* in September 2001, but each called during both years of the study. *Smilisea baudinii* was only encountered during July and August 2001..

Species began calling prior to the pool filling with water. The number of species calling peaked at six during August 2000 and again in July 2001. Five species called during both years of the study *(Agalyehnis eallidryas, Hyla microeephala, Hyla pieta, Scinax staufferi,* and *Leptodaetylus melanonotus). Bufo valliceps* called at index 1 only during August 2000 and *Gastrophryne elegans* called at index 1 only during July 2001. No observations of breeding activity were recorded in 2000, but in 2001, *A. callidryas* egg masses were observed in July and *Smilisea baudinii* eggs were found in August.

Savanna 100 m Site

The pools at the Savanna 100 m Site were filled during every survey (Fig. 11). A total of 10 species were reported (Table 5) and breeding observations were reported for five species. The number of species encountered ranged from zero to three each month, while the number calling varied between zero and four (Appendix 7).

Species were encountered during the months of May, June, and October to December in 2000 and during January, February, June, July, and October 2001. Four species *(Bufo valliceps, Smilisca baudinii, Rana berlandieri,* and *Leptodactylus labialis)* were encountered during both years of the study. Two species were visually observed during only one month, one individual of *Bufo marinus* during July 2001, and one individual of *Scinax staufferi* during May 2000. Individuals of *Rana vaillanti* were only encountered during November 2000 to January 2001.

The Savanna 100 m Site typically had more species calling early in the wet season, perhaps because fish often invaded these pools as the wet season progressed. The number of species calling peaked at four in May each year, then declined in number until October when only *Hyla picta* remained calling. Five species called during both years *(Bufo valliceps, Hyla picta, Scinax staufferi, Smilisca baudinii,* and *Leptodactylus labialis).* Three additional species called during 2001 at inetex 1, *Hyla microcephala* during May, and *Rana berlandieri* and *Leptodactylus melanonotus* during July. Observations of breeding were not frequent at this site, with eggs of S. *baudinii* found during May 2000, eggs of *R. berlandieri* found in July 2001, and tadpoles of *B. valliceps* in September 2001. In addition, metamorphs of *R. berlandieri, R. vaillanti,* and *L. labialis* were observed.

Savanna Site

The temporary pool at the Savanna Site was filled with water from June to December in 2000, and during February and from June until the end of the study in 2001 (Fig. 11). Total species richness at the site was five, with observations of breeding for only two species (Table 5). The number of species visually observed ranged from zero to two species each month, while the number calling ranged from zero to three (Appendix 8).

Species were encountered at the Savanna Site from April until October 2000 and during January and July of 2001. Two species were visually observed only during 2000, including one individual of *Bufo valliceps* reported in July and individuals of *Rana berlandieri* observed during September and October. Sightings of *Leptodactylus labialis* occurred during May, June, and October in 2000 and during January 2001, but this species was not observed during the wet season in 2001.

Fish often invaded the Savanna Site pool as the wet season progressed and this possibly influenced calling activity, which occurred mainly during the beginning of the rainy season. Species called during the months of May to September in 2000 and during May, July, and August in 2001. Calling peaked with three species in June (*Hyla microcephala, Scinax staufferi*, and *Leptodactylus labialis*) and July (*S. staufferi, Rana berlandieri*, and *L. labialis*) in 2000. The site was not as active during 2001, with two species calling during May and June (*H microcephala* andS. *staufferi*), and one (*S staufferi*) calling during August. *L. labialis* called in large choruses of over 50 individuals during May and June 2000 and at index 2 during July, yet it was not heard calling in 2001. Individuals of the genus *Rana* called in May and July of 2001, but it could not be confirmed whether it was *R. berlandieri* or *Rana vaillanti*. Observations of breeding activity for *R. berlandieri*, in the form of an egg mass in July, and *1. labialis*, in the form of metamorphs in August and September, were reported in 2000 but no observations of breeding were reported in 2001.

Disturbed Site

Observations of activity at the Disturbed Site were less complete than at the BNR sites due to low sampling effort. Water was only present in the site during the wet season months. Total species richness was seven but observations of breeding activity were not recorded for any of the species (Table 5). The number of species visually observed ranged from zero to four per survey, while the number calling ranged from zero to five (Appendix 9).

Visual encounter and/or calling observations were made during August 2000 and May and August 2001, three of the five months when surveys were conducted. Three species were only observed during May 2001, one *Rana berlandieri* visual observation and two species, *Bufo marinus* and *Bufo valliceps,* which were encountered and calling. Four species (*Hyla microcephala, Scinax staufferi, Smilisca baudinii*, and *Leptodactylus melanonotus*) were observed visually or calling during both years.

Summary

Three trends emerge when comparing annual species activity and abundance at the nine study sites. First, a greater number of species were active earlier in the wet season at the Base of Hill Site and Forest Entrance Site in 2001 compared to 2000. Second, more observations of breeding activity for a greater number of species were reported during 2001 than in 2000, particularly at the Base of Hill Site, Forest Entrance

Site, Forest Pool Site, and Transition Pool Site. Third, *Hyla picta, Scinax staufferi*, and *Leptodactylus labialis* called in greater numbers during more months in 2000 than in 2001.

Two patterns emerge when comparing species activity during the wet season at different site locations. First, more species were observed earlier in the wet season at the road sites in comparison to the off road sites. Second, breeding was concentrated at the beginning of the wet season at the Savanna 100 m Site and Savanna Site.

Species Accounts

It is worthwhile to examine each species separately in order to highlight behavior and activity patterns observed during the study. The following accounts present data on temporal and spatial distributions and breeding activity observed for each species during the study period. This section will include activity at ~ltes as well as opportunistic observations along the road and trails. It is important to remember that the data on tadpoles and metamorphs were not measured by formal methods. Therefore, the data presented on those life stages is not exhaustive.

Bufo marinus

Bufo marinus was observed during every month of the study except December 2000 (Fig. 10). It vocalized during both wet and dry seasons nearly every month, but particularly avoided calling activity during May and June. Calling indices never exceeded 2 (6 – 20 individuals). Presence of eggs and/or amplexus were only observed during March 2000 and September 2001 (Fig. 10; Table 3). Tadpoles were observed during April and September through November 2000 and in October 2001. This indicated that breeding was more frequent than directly observed by eggs or amplexus, given that the average time to metamorphosis is a few weeks (Meyer and Foster, 1996).

Bufo marinus was encountered regularly at the Bladen River Crossing Site, the only site where it was found breeding. It was also observed at sites along the road, Forest Entrance Site, Base of Hill Site, and Savanna 100 m Site, but at no sites off the road (Table 5). It is interesting to note that the months when *B. marinus* was not calling at the river (May and June both years) were the same months it was found at the Base of Hill Site and Forest Entrance Site, in addition to other temporary pools along the road. Although not observed, it is expected that these individuals were taking advantage of the large breeding congregations and the tadpole populations of other species as a food source during these months. Typically one *B. marinus* individual was present at each temporary pool, as if demonstrating territorial behavior.

In August 2001, individuals were calling at a pool in the floodplain of the river. It is uncertain whether *Bufo marinus* breeds in pools with other species (J. Campbell, pers. comm.) and observations during this study suggest that it may. *Rana berland~eri* was observed breeding in this same pool a month later and *Bufo valliceps* bred there in July 2001.

In summary, *Bufo marinus* can be classified as a species that breeds periodically throughout both the wet and dry seasons. It was only encountered at the Bladen River Crossing Site or at sites along the road, indicating that it prefers more open canopy locations with shallow temporary pools.

Bufo valliceps

Bufo valliceps was one of the most commonly encountered species during the study (Table 5). It was observed during every month except April and October 2001 (Fig. 10). During April this may have been due to low sampling effort, as surveys were only conducted on one night. *B. valliceps* began calling when precipitation increased at the beginning of the wet season and continued calling for about four months (Table 3), declining before the end of the rainy season. Reported calling indices were usually 2 or 3; one calling index of 4 was reported during August 2000. Evidence of amplexus and/or eggs was found from June to September in 2000 and May to July in 2001 (Table 3). Tadpoles and/or metamorphs were observed from April to November in 2000 and from May to September in 2001.

Bufo valliceps was observed at every site except the Forest Pool Site; however, it was only observed breeding in sites or other pools along the road or at the river (Table 5). It was an opportunistic breeder and some nights would be found in breeding congregations in almost every roadside pool. *B. valliceps* was observed calling in a pool in the floodplain of the Bladen River Crossing Site during May, July, and August in 2001. Although it was the most common species found in the leaf litter of the Forest Site, breeding was never observed.

In summary, *Bufo valliceps* can be regarded as an abundant, habitat generalist. It is tolerant of disturbed locations. It is important to note that on occasion *B. valliceps* may have been incorrectly identified. *Bufo campbelli*, a species recently distinguished from *B. valliceps*, is known to occur in this area of Belize. However, since *B. campbelli* is only known to breed in streams, it is unlikely that the breeding observations of *B. valliceps* are incorrect (Campbell, 1996; Lee, 2000).

Agalychnis callidryas

Agalychnis callidryas was observed during the first 3 or 4 months of the wet season (Fig. 10). Each year, it began calling at index 1 or 2 during May and peaked in July at index 3 or 4 (Table 3; Fig. 10). After the peak month, calling declined but continued both years until late in the wet season. In 2000, 1 - 5 individuals were still calling in December. Egg masses or amplexus were observed during July and August of 2000 and from May to September of2001 (Table 3). Donnelly and Guyer (1994) described *A. callidryas* as a persistent wet season breeder based on its activity in a pool at La Selva, Costa Rica; this description was also fitting of its behavior during this study.

Agalychnis callidryas was observed calling and breeding in most of the forest habitat sites, including the Transition Pool Site but excluding the Forest Site. It was also encountered at locations along the road in the forest.. Once the pool was able to maintain water, the Forest Pool Site consistently had the highest number of individuals of *A. callidryas* in calling congregations (Appendix 5). This species was typically encountered while calling perched on woody vines, tree branches, or heli~onia plants at heights of 241 ± 25 cm (mean ± SE, n = 44). This was greater than perch heights (approximately 160 ± 14 cm (mean ± SE)) reported for *A. callidryas* at La Selva, Costa Rica (Donnelly and Guyer, 1994). Yet in both the present study and that of Donnelly and Guyer (1994)*A. callidryas* perched at greater heights than other hylid species. Occasionally *A.. callidryas* would call at heights over 4 m in the canopy, presumably an indication that it was not actively breeding. Yet, egg masses, usually on the underside of leaves over water, were found at a great range of heights, 15 – 600 cm (192 ± 81 cm (mean ± SE), n = 7); all except one of these egg mass measurements were collected at the Transition Pool Site during 30 July to 1 August 2001. Therefore, *A. callidryas* may commonly lay egg masses at heights above that which would be easily observed. Donnelly and Guyer (1994) reported that *A. callidyas* laid its egg masses at heights of 110.2 ± 6.98 cm (x ± SE, n = 136) at La Selva. There was much more variation in heights of egg masses found in the present study. Other exceptions to the typical patterns include one survey night when two *A. callidryas* individuals were observed in amplexus creeping along the road. In addition, egg masses were sometimes observed on vegetation in locations that lacked standing water, perhaps laid in expectation that a pool would fill before the eggs hatched.

In summary, *Agalychnis callidryas* called continuously during the wet season, but the number of individuals calling declined during the latter half of the season. This arboreal, nocturnal species retreated into the canopy during the dry season. *A. callidryas* can be regarded as a habitat specialist, exclusively found in sites with high canopy cover and typically low vegetation height (Fig. 14 & 15).

<u>*Hyla ebraccata*</u>

Hyla ebraccata was one of the least commonly encountered species during this study. It was only heard calling during a few months and was rarely observed (Fig. 10). *H. ebraccata* began calling and peaked at index 2 in July each year (Table 3). In 2000, calling individuals were heard through September; however, in 2001, calling was only heard in July. No evidence of breeding was recorded during the study, but it was suspected that successful breeding did occur. In August 2000, hylid egg masses were observed but could not be confirmed to be that of *H. ebraccata* due to their similarity with other hylid species. The patterns reported for *H. ebraccata* in this study were much different from that observed for the species at a temporary pool in La Selva Biological Station in Costa Rica (Donnelly and Guyer, 1994). At La Selva, *H. ebraccata* was characterized as an abundant species and a persistent breeder, peaking in numbers early in the wet season.

Hyla ebraccata was only observed at the Base of Hill Site, Forest Entrance Site, and Forest Pool Site (Table 5), all sites that had a closed canopy and low vegetation height (Fig. 14 & 15). The site where they were observed in the highest concentration both years was the Forest Pool Site (Appendix 5). *H. ebraccata* perched on vegetation over water at low heights, 30 ± 10 cm (mean ± SE, n = 2), similar to heights reported by Donnelly and Guyer (1994), approximately 33 ± 3 cm (mean ± SE).

In summary, *Hyla ebraccata* demonstrated a delayed start in calling activity during the wet season and had a very short breeding season (1- 3 months) (Table 4; Fig. 10). Thereafter the species returned to the canopy and was not usually observed until the following wet season. One exception to this pattern occurred on 25 April 2000, the driest month of the study, when one individual of *H. ebracccata* was observed at the Base of Hill Site exposed on the soil surface. Overall, it can be regarded as an uncommon, nocturnal, habitat specialist of lowland forests.

Hyla loquax

Hyla loquax became active in July, a couple months after the rainy season began, comparable to the pattern reported for this species at La Selva, Costa Rica (Donnelly and Guyer, 1994). In the present study *H. loquax* was encountered during July each year, in addition to August and September in 2000 and May in 2001 (Fig. 10). It called at index 3 or 4 in July both years, then decreased in calling intensity each month until October, when calling ceased (Table 3). In July 2001, amplexing individuals were observed and egg masses, presumably of this species, were located. Fortunately, tadpoles of *H loquax* were easily identified in the field and were observed in August and October of 2000 and in August of2001 (Fig. 10).

Hyla loquax was found exclusively at the Base of Hill Site, Forest Entrance Site, and Forest Pool Site (Table 5), all sites with a closed canopy and low vegetation height (Fig. 14 & 15). A calling index of 4 was recorded during July and August 2001 at a location close in proximity to the Forest Pool Site. *H loquax* perched on the upper half oftall grass blades and various herbaceous vegetation (86 ± 16 cm, mean ± SE, n = 13), similar to heights reported at a pool in La Selva, Costa Rica (approximately 70 cm ± 4; mean ± SE) (Donnelly and Guyer, 1994).

In summary, breeding activity of *H loquax* was observed during three months, July to September, at the height ofthe rainy season each year (Table 4). This species can be regarded as a common, nocturnal, specialist ,of lowland forests. It is also known to occupy savanna habitat (Lee, 2000; Meyer and Foster, 1996), but was not found in savanna sites during this study.

<u>Hyla microcephala</u>

Hyla rnicrocephala was encountered during five to six months each rainy season and began calling in May each year (Fig. 10). In 2000: calling peaked at index 4 in July, then declined each month until calling ended after September (Table 3). In 2001, calling peaked in May and July at index 4, then calling declined each month but was still heard in October. This species vocalized for a long duration each wet season but was not active during the dry season (Table 4). One exception to this pattern was three *H microcephala* individuals observed in the stem and leaf folds of wild cocoa plants at the Base of Hill Site during April 2000. Egg masses, presumably of *H microcephala,* were observed in July 2000 and amplexus was observed in May and July 2001 (Table 3; Fig. 10). Tadpoles were only found in October 2000.

Hyla microcephala was encountered at every site except the Bladen River Crossing Site and Forest Site, and was also found at many temporary pools along the road (Table 5). It did not exhibit a specific habitat preference, ranging from sites with a closed to open canopy and high to low vegetation heights (Fig. 14 & 15). Although it required vegetation for perching, it did not seem to exhibit a preference in vegetation type, perching at low heights (48 ± 4 cm, mean ± SE, n = 80) on grass blades, palm fronds, or various herbaceous plants.

Overall, *Hyla microcephala* was a common, nocturnal anuran, general in its habitat requirements and active throughout the wet season. It was one of the three hylid species encountered in the Disturbed Site, reflecting its ability to handle variable environmental and climatic variables.

Hyla picta

Hyla picta was patchy in its presence and calling consistency. It was visually encountered during May and July each year, in addition to August in 2000 (Fig. 10). Calling was first heard in May 2000 and then peaked at index 3 in August (Table 3). Then calling declined each month until it ceased after October 2000. In 2001, calling peaked in both May and July at index 4 and then index 1 was recorded from August to

October.. No calling was heard in June of either year; in 2001 this may be due to little precipitation. No observations confirming breeding activity were made.

The majority of observations of *Hyla picta* were in transitional habitat between the forest and pine-savanna habitats along the road and at the Transition Pool Site and Savanna 100 m Site, although it was occasionally encountered in forest sites (Table 5). Calling was heard in May 2000 at the Forest Site despite the lack of standing water within the site (Appendix 4). Interestingly, this species was not observed or heard again in the near vicinity until May 2001 when it was observed and calling at the Base of Hill Site and Forest Entrance Site. All of the sightings of *H picta* in forest habitat sites occurred during the beginning of the rainy season. In constrast, at the Transition Pool Site and Savanna 100 m Site, this species demonstrated a late onset in breeding activity each year (Appendix 6 & 7). Overall, it seemed to prefer breeding in grassy patches with an open canopy (Fig. 15) and was typically encountered perching on grass blades when calling.

In all, *Hyla picta* was common during aJew short episodes during the study period. It was nocturnally active, exclusively during the wet season, and seemed to be specific in its selection of savanna breeding habitat, yet general in its presence (Fig. 14 & 15).

Scinax staufferi

Scinax staufferi was primarily active during the wet season; yet, i~was heard calling once during the dry season in February 2001 (Table 3; Fig. 10). In 2000, calling peaked at index 4 during May and August and was at index 3 during June and July. Calling activity declined in September, after which it ceased (Table 3). In 2001, calling began in May but then was much different from the pattern observed in 2000. Calling peaked in July at index 3 when standing water was persistent in the temporary pools, but by September 2001 calling had ended. Smaller breeding congregations were observed in 2001 in comparison to 2000. No direct observation of breeding was made in either year.

Scinax staufferi called on one survey at the Forest Entrance Site and at the Forest Pool Site early in the wet season (Appendix 3 & 5; Table 5). However, this species seemed to prefer open canopy habitat with high vegetation growth, as it was more abundantly observed calling and suspected to be breeding within savanna habitat (Fig. 15). The high calling indices observed during 2000 were at the Savanna 100 m Site and Savanna Site (Appendix 7 & 8). S. *staufferi* typically perched on grass blades or the trunk of a pine tree when calling. Individuals were visually observed and/or vocalizing at the Disturbed Site during three surveys.

In summary, *Scinax staufferi* became active early in the wet season and its breeding activity was confmed to four months (Table 4). It can be described as an abundant, nocturnal anuran, typically found in open habitat and tolerant of disturbed situations.

Smilisca baudinii

Smilisca baudinii was commonly encountered during the wet season and was occasionally observed during March and April in the dry season (Fig. 10). Calling began in May, typically occurring with the fIrst rains, and continued for fIve months each year (May to September) (Table 3). S. *baudinii* occasionally demonstrated explosive breeding behavior and sometimes called during the day, especially at the start of the rainy season. For instance, one large breeding congregation (100+ individuals) was observed calling until after 9:00 h on 28 May 2001 in an open grassy area near the Forest Pool Site. S. *baudinii* was characterized as an explosive breeder by Donnelly and Guyer (1994) at La Selva in Costa Rica. However, this breeding strategy was not regularly demonstrated in the present study. Evidence of breeding was observed during many wet season months in the form of easily distinguishable eggs that are laid as a thin layer across the water surface (Fig. 10).

Smilisca baudinii was encountered at every site except the Savanna Site, although it almost exclusively bred only at sites or other temporary pools on the road (Table 5). This species usually congregated on the ground at edges of the water in small breeding populations, but it was also found perching on vegetation above the ground. In December 2000, one adult was observed on a dead log at the Bladen River Crossing Site. A small pool underneath the log had tadpoles that were presumed to be S. *baudinii.*

In summary, *Smilisca baudinii* called during five months each wet season (Table 4). It was an abundant species and a habitat generalist.. However, it seemed to breed most regularly at small temporary pools in locations with variable canopy cover and some vegetation growth (Fig. 15).

Smilisca cyanosticta

Smilisca cyanosticta was only observed on one occasion during the study period. On 30 August 2001 it was found resting at the edge of a temporary pool on the road within 200 m of the Base of Hill Site. The observation of this species was peculiar given that it is only known to occur at higher elevations (167-667 m) (Meyer and Foster, 1996). However, it was possible that the specimen was swept down the river from a higher elevation during a heavy rain. Additional research will be necessary to confirm the presence of this species within the area.

Gastrophryne elegans

In April 2000, 10 individuals of *Gastrophryne elegans* were encountered during one survey at the Base of Hill Site and 17 individuals were encountered at the Forest Entrance Site (Table 3; Appendix 2 & 3). Individuals were also visually observed at several other locations along the road and this abundance was unusual given that April 2000 was the driest month of the study. The only other month this species was observed was during August 2000. Vocalizing individuals were not heard during 2000. During 2001, calling was heard at index 2 during May off the roadside and in July index 1 was recorded at the Transition Pool Site (Fig. 10; Appendix 6). Tadpoles of *G. elegans* were easily identified and observed in large numbers at the Forest Pool Site from July to September 2001 (Table 3; Fig. 10).

Gastrophryne elegans was only encountered in forest habitat sites, with a closed canopy and low vegetation height (Fig. 14; Table 3). In addition, evidence of breeding during more than one survey was only found at the Forest Pool Site (Fig. 15).

In summary, *Gastrophryne elegans* called sporadically and somewhat explosively after heavy rains early in the wet season, probably breeding during only two months each year (Table 4). It was an uncommon, nocturnal species that specialized in forest habitat with a closed canopy. As recently as 1996, *G. elegans* was only known from a few observations in Belize (Meyer and Foster, 1996), but in the years during this study it was regularly reported from sites around the country.

Rana berlandieri

Rana berlandieri was observed along the road during almost every month of the study (Table 3; Fig. 10). This species was found near or in temporary pools by day and night. The number of individuals encountered increased once the rains began in May. The first calling individuals were observed in July 2000 and calling continued each month through September. Typically only 1 – 5 individuals would call at a site, but on one occasion (30 July 2001) a breeding congregation of 16 individuals was observed at a roadside pool. Egg masses were found from July to September and in December 2000, and metamorphs were first encountered in September along the road. The following year, calling and egg masses were observed from May to July and in October (Table 3).

This species was encountered at all sites except the Forest Site and Forest Pool Site (Table 5). In October 2001, *Rana berlandieri* individuals and egg masses were observed at the pool in the floodplain of the r~ver. However, this species seemed to prefer small, shallow, temporary pools in sites with some canopy cover and emergent vegetation for its eggs to attach to (Fig. 15).

In summary, *Rana berlandieri* called during three months each wet season, although it was suspected to be a more frequent breeder due to its sporadic calling nature and the confirmation of egg presence during four months each year (Table 4). It was not heard calling during the dry season nor were tadpoles or metamorphs observed, although it has previously been reported to breed during the dry season in other areas of its range (Campbell, 1998). *R. berlandieri* was a common, diurnal and nocturnal species, and a habitat generalist.

Rana vaillanti

Rana vaillanti was encountered almost every month during the study; however, calling and breeding were never directly observed (Table 3; Fig. 10). Eggs and tadpoles that were presumed to be *R. vaillanti* were observed from July until November 2000 (Table 3). Metamorphs were observed each month from August until December 2000; however, in 2001, metamorphs were only observed in October.

Rana vaillanti was encountered in every site except the Savanna Site, Forest Site, and Disturbed Site (Table 5). It was commonly observed at the Forest Pool Site laying motionless on the water surface until disturbed.

In summary, the breeding activity of *Rana vaillanti* was difficult to observe due to its particularly wary nature. It seemed to prefer forest habitat with a closed canopy (Fig. 14); although, it could be found on the edges of this habitat.. It was a common, dirumal and nocturnal, terrestrial anuran.

Leptodactylus labialis

Leptodactylus labialis was observed throughout the year, often jumping from the edge of a pool into water when disturbed (Fig. 10). Calling was heard by day and night, reaching a maximum calling index of 4 in May and June 2000 in the Savanna Site (Fig. 10; Appendix 8). Metamorphs were observed from June to September and in November 2000 and during January 2001. Therefore, it was likely that breeding took place more frequently than determined by calling observations alone. In 2001, calling peaked at index 3 in May and was only heard during two additional months, June and August at index 1 (Table 3). Metamorphs were only found in September 2001. *L. labialis* was encountered and heard calling less frequently during 2001 than in 2000.

Leptodactylus labialis was most commonly encountered at the Savanna 100 m Site and Savanna Site and along the road in the savanna, yet it was observed on two survey months at the Base of Hill Site (Table 5). Nevertheless, it demonstrated a definite preference toward sites with an open canopy and high vegetation height when breeding (Fig. 15).

In summary, *Leptodactylus labialis* was primarily active from May to August, early in the wet season (Table 4). It was a common species, active by day and night, and specialized in savanna habitat. *L. labialis* was often difficult to observe when vocalizing, since it positioned itself in borrows at the sides of temporary pools or at the base of grasses. Interestingly, this species was especially abundant at the Savanna Site during May and June 2000, even though fire had consumed the site during the previous April.

Leptodactylus melanonotus

Leptodactylus melanonotus was encountered periodically during the study throughout the year (Fig. 10). It began calling in June 2000 at index 2 during the day and night and continued in a similar manner until October (Fig. 10; Table 3). In December 2000, an immature individual was observed near the Transition Pool Site. Then there were no observations until April 2001 when several individuals were observed at the Forest Entrance Site with tadpoles. Calling peaked at index 2 in July 2001 and continued through October at index 1 (Fig. 10).

Leptodactylus melanonotus was encountered at every site except the Bladen River Crossing Site, Forest Site, and Savanna Site (Table 5). It did not appear to demonstrate specific preferences in habitat type and was tolerant of open canopy sites with little vegetation (i.e., Disturbed Site). A notable sighting of this species took place at the

Transition Pool Site in September 2001. One adult seeming to demonstrate parental care was observed resting on leaf litter near a group of schooling tadpoles.

In summary, *Leptodactylus melanonotus* was an active caller during four months each rainy season beginning in June or July, and it likely bred during four months each year (Table 4). Some evidence was found indicating that this species may breed during the dry season, but further research is needed to confirm this. *L. melanonotus* was a common, habitat generalist and active both by day and night. It was difficult to observe because of its habit of hiding underneath leaf litter while calling.

Rhinophryas dorsalis

Rhinophryas dorsalis, an explosive breeder after heavy rains early in the wet season (Meyer and Foster, 1996), called at index 3 on 18 May 2000 at the Forest Entrance Site (Table 3; Appendix 3). Amplexing individuals were observed this same night and tadpoles were found in the pools the following day, indicating that breeding had already occurred. A heavy rain on 6 May 2000 may have induced this breeding. In June 2000, tadpoles were observed and one adult encountered on the road in transitional habitat. There were no further observations until May 2001, when calling was observed at index 1 (Fig. 10). Sporadic individual calls were heard at ~ifferent locations in June 2001. Tadpoles were ab~dant in the Forest Pool Site during July and August 2001 (Fig. 10).

Rhinophryas dorsalis was only observed in the Base of Hill Site, Forest Entrance Site, and Forest Pool Site (Table 5), all sites with a closed canopy (Fig. 14 & 15). However, this species has also been reported to also commonly occur in savanna habitat (Lee, 2000).

In summary, *Rhinophryas dorsalis* was a noctural, fossorial anuran, demonstrating explosive breeding activity early in the wet season (Table 4). It was important to search for *R. dorsalis* during the first heavy rains of the season, since it was very difficult to observe during the rest of the year.

Summary

There are several trends that appear when examining the activity of species in BNR. Species partition their activity in a temporal manner by use of different breeding strategies (continuous vs. explosive), seasons, and duration of breeding. Partitioning of space is demonstrated by comparing habitat generalists and specialists and species preference for specific microhabitat within a site. These patterns lead to the community structure and composition observed at anyone time at a site.

Some species were commonly observed in ass~Ciation with another species even at different times of the year or at different sites. *Scinax staufJeri* was usually encountered in association with *Leptodactylis labialis,* expecially at the Savanna 100 m Site and Savanna Site early in the wet season. *Rana berlandieri, Rana vaillanti, Bufo valliceps, Smilisca baudinii, and Hyla microcephala,* all common habitat generalists, were typically encountered in sites together, especially along the road Although, at the Forest Pool Site where *R. vaillanti* was found regularly, *R. berlandieri* was never encountered.

DISCUSSION

Species Richness

A total of sixteen anuran species were encountered at the Bladen Nature Reserve sites. In contrast, only seven species were found at the Disturbed Site. Additional species are known to occur in the area surrounding the study sites in BNR including *Eleutherodactylus sabrinus, Hyalinobatrachium fleischmanni,* and *Bufo campbelli* (Lee, 2000; J. Arrigoni, pers. comm.); however, they are usually encountered at streams, a habitat not included in this study. Approximately 26 ofthe 33 anuran species known from Belize are expected to occur within BNR based on range maps (Lee, 2000). Several of these species only occur at elevations over 100 m, again, an area not surveyed in this study.

It is generally understood that anuran diversiti~is negatively correlated with latitude and altitude and positively correlated with annual rainfall and equitability of rainfall throughout the year (Duellman and Trueb, 1994). So not surprisingly, studies at Central American sites south of Belize report a higher number of species than found in the present study. Twenty-three species were observed at one temporary pool in La Selva Biological Reserve in Costa Rica (Donnelly and Guyer, 1994), with 44 species reported from the entire reserve (Scort et aI., 1983), and 30 species were reported from Barro Colorado Island, Panama (Rand and Myers, 1990). Even higher species richness was reported for adult anurans at locations in South America with 46 species at seven aquatic breeding sites in Panguana, eastern Peru (Aichinger, 1987); 48 species at six breeding sites at Fazenda Intervales in southeastern Brazil (Bertoluci, 1998); 37 species in four forest types in the lower Amazon Basin of Brazil (Crump, 1971); and 81 species from Santa Cecilia, Ecuador (Duellman, 1978).

Some of these more speciose sites have comparable annual precipitation to BNR (mean = 2428 mm from 1997 – 2000) including the lower Amazon Basin of Brazil with 2858 mm (Crump, 1971) and Panguana, eastern Peru with 2634.6 mm (Aichinger, 1987), both seasonal sites. Others have comparably lower annual precipitation such as Fazenda Intervales, a seasonal site in southeastern Brazil with 1755.6 mm (Bertoluci, 1998), or higher annual precipitation with 4000 mm reported at La Selva, Costa Rica, a semi-seasonal site (Donnelly and Guyer, 1994), and 4400 mm reported at Santa Cecilia, Ecuador, an aseasonal site (Duellman, 1978). It is obvious when comparing these sites that species richness increases with a decrease in latitude and with aseasonality in rainy tropical environments. This is partially because the climate varies little and therefore is more conducive to year-long activity. Species have adapted by partitioning their habitat to a greater degree and by evolving elaborate reproductive modes. For example, in Santa Cecilia, Ecuador (Duellman, 1978), more species are active by day, such as species of dendrobatids, and throughout the year than at BNR. Species of the genus *Eleutherodactylus*, which are able to undergo direct development, are especially speciose close to the equator. In contrast, all of the species observed in the present study require standing water for reproduction. The bufonids and ranids lay their eggs directly in water, in strings (Lee, 2000) and masses respectively. Leptodactylids lay their eggs in foam nests near or at the edge of water (Lee, 2000). The single rhinophrynid and microhylid lay their eggs directly into the water and the hylids lay their eggs either in egg masses on vegetation above the water or as a surface film on the water (i.e., *Smilisca*) (Lee, 2000;

Meyer and Foster, 1996. In summary, this study fits with the large-scale trend in species richness as predicted by latitude and seasonality.

Temporal Distribution of Anuran Activity

Precipitation

In southern Belize, a region with a pronounced dry season, anuran activity was highly influenced by precipitation and the related variable of water permanency. A few species were encountered throughout the year, but observations of reproductive activity increased sharply with the start of heavy rains in May. This pattern is similar to that found in other seasonal tropical locations (Donnelly and Guyer, 1994; Aichinger, 1987; Crump, 1971; Gascon, 1991). Yet as mentioned, with a decrease in latitude more species are able to breed independent of aquatic sites because of increased ambient humidity, so breeding is somewhat more equally distributed throughout the year. For example, six species at Panguana in eastern Peru do not require standing water to breed (Aichinger, 1987), but breeding still demonstrates a rise in the beginning of the rainy season. At an aseasonal site such as Santa Cecilia, Ecuador, 21 of 81 species did not require standing water for reproduction; however, Duellman (1978) still emphasized that anuran breeding activity was positively influenced by rainfall..

Two months of the study period appeared atypical fmm the normal dry/wet season cycle. June 2001, an unusually dry month (total precipitation = 72.5 mm versus mean = 466.2 mm from 1997 - 2001), provided evidence for the close correlation between anuran activity and rainfall.. Activity declined in June, with fewer species being directly observed or vocalizing than in the previous May, which had more typical rainfall. However, despite this dry spell, an equal number of species called as in the previous June

2000 and considerably more species were active than during dry season months with comparable precipitation. This leads one to believe that anurans were influenced by factors other than precipitation. Most of the active species (i.e., *Bufo valliceps*, *Agalychnis callidryas*, *Hyla microcephala*, *Scinax staufferi*, *Smilisca baudinii*, *Rana berlandieri*, and *Leptodactylus labialis*) were habitat generalists and continuous breeders and possibly had a higher tolerance to variation in abiotic factors such as precipitation. Therefore, as long as some pools of water were available these species were prompted to breed regardless of actual precipitation amounts early in the wet season. Variation in rainfall also did not affect breeding activity of continuous breeders in Brazil (Gascon, 1991) and in another study continuous breeders were concluded to have higher tolerance to variations in climate (Bertoluci, 1998), agreeing with the results of this study.

The other atypical month was April 2000, the driest month of the study (total precipitation = 9.6 mm vs. mean = 47.5 mm from 1997 - 2001). This time period was when nine species were observed at the Base of Hill Site, including 10 individuals of *Gastrophryne elegans* (a species which was found not during any other survey at this site) during one survey. In addition, 17 individuals of this same species were observed at the nearby Forest Entrance Site this month, again the only observations of *G. efegans* at the site during the study. A tractor had moved sediment in attempts to flatten the road during April and many of the *G. elegans* individuals were observed amongst the clumps of overturned soil. Perhaps this disturbance stimulated *G. elegans* to become active. However, this event does not explain why several other species were observed, including *Hyla ebraccata* and *Hyla microcephala*, which would be expected to be secluded in the forest canopy at this time of year. It is possible that the Base of Hill Site provided greater relative humidity than the surrounding area, since it was indeed at the base of a hill. High diurnal temperatures and lack of rain may have given some hylid species no choice but to leave their retreat sites and descend to the forest floor, hoping to rehydrate themselves. Other species may have become active in anticipation of the coming rains.

Breeding strategies and duration

Temporal differences in species activity were evident when examining breeding strategies and duration. Eight species exhibited continuous breeding activity for four to five months of the wet season *(Smilisca baudinii, Hyla microcephala, Bufo valliceps, Scinax staufferi, Leptodactylus melanonotus; Rana berlandieri, Agalychnis callidryas,* and *Hyla picta),* and two of these species (S. *baudinii* and *B. valliceps)* could also be described as opportunistic breeders. The opportunistic strategy involved laying numerous egg clutches in temporary pools, in the hopes that some would be successful (Heyer et al., 1975). In contrast, two species could be characterized as explosive breeders early in the wet season *(Rhinophryas dorsalis* and *Gastrophryne elegans).* Three species exhibited a short breeding duration beginning early or late in the wet season *(Hyla ebraccata, Leptodactylus labialis,* and *Hyla loquax)* and one species *(Bufo marinus)* bred during both the wet and dry seasons. Gascon (1991) suggested that species use time as well as rainfall as a cue for the onset of reproduction. Perhaps, time was used by species exhibiting a late onset in this study (i.e., *H ebraccata* and *H loquax);* this strategy may be an adaptation in species that prefer to breed at temporary pool sites since they can suffer heavy mortality from desiccation if they become active earlier in the season when water permanency is less predictable. The breeding strategies used by species in this study resulted in the peak number of active species occurring in July, two months after the rainy season began, a time of more predictable water permanency at temporary pools.

Anurans utilizing certain breeding strategies differed by site. For example, explosive breeders were not present at the Savanna 100 m Site, Savanna Site, and Disturbed Site. Most of the species present at the Savanna 100 m Site, Savanna Site, and Disturbed Site were characterized as prolonged or opportunistic breeders yet they did not demonstrate as lengthy a breeding period in comparison to the forest sites. This may be due to water permanency and predation as explained in the following section.

Diurnal anuran activity was not very commonly observed in this study. *Leptodactylus labialis, Leptodactylus melanonotus, Rana vaillanti, Rana berlandieri, and Bufo valliceps* were occasionally active and/or vocalized by day as well as at night; however, most species were exclusively active at night.. Diurnal activity was more common in forest habitats than in the savanna. Lack of canopy cover resulting in high temperatures combined with low relative humidity by day in the savanna sites would certainly deter anurans from activity since they are prone to dessication. In comparison, at Santa Cecilia, an aseasonal site in Ecuador, Duellman (1978) reported 11 species, all specialists of forest habitats, to be strictly diurnal and eight species to be active by day and night..

Agalychnis callidryas demonstrated a longer calling period than that presumed for actual breeding and it is possible that other hylid species had similar behavior. This has been reported for hylid species at other locations (Donnelly and Guyer, 1994; Crump, 1971) and the authors caution about the connection between calling and reproductive activity in these frogs.

Usually one species would seem to be the dominant caller on a given night at a site. In particular this was observed between *Hyla microcephala* and *Hyla loquax*. They seemed to avoid overlap in calling activity at the same site on the same night, perhaps due to competition for calling sites, although *H loquax* typically perched higher than *H microcephala*. *Smilisca baudinii* and *Bufo valliceps* were commonly active together on nights after heavy rains, often when other anurans such as *H microcephala* and *H loquax* were not active. Additional research is required to better understand this behavior. This pattern may be more obvious at sites with higher species richness (e.g. Crump, 1971). Additionally, temporal partitioning ofthe habitat may allow more species to utilize a pool by decreasing competition during the aquatic stage (Crump, 1971).

Summary

In summary, rainfall seems to be the most important abiotic factor influencing breeding activity at BNR sites. Different strategies, durations, and seasonality of breeding, as well as avoidance of calling overlap are ways that species seem to partition their resources on a temporal level at the study sites in BNR: Temporal patterns in species breeding activity would be more clear if surveys were conducted weekly at each site and if tadpole assemblages were studied more thoroughly.

Spatial Distribution of Anuran Activity

Water permanency and habitat preferences infl~enced the annual activity, habitat use, and community structure of anurans. Sites varied across gradients in abiotic factors such as humidity, temperature, and water permanency as well as vegetation characteristics such as canopy cover, vegetation height, and vegetation types.

Water permanency

Water permanency directly influenced species activity and presence at sites since reproduction of all species encountered was dependent on water.. The three road sites (Base of Hill Site, Forest Entrance Site, and Savanna 100 m Site) and the Bladen River Crossing Site had semi-permanent or permanent water presence during the study, whereas the four sites off ofthe road (Forest Site, Forest Pool Site, Transition Pool Site, and Savanna Site) and the Disturbed Site had temporary pools that only filled during the wet season. Water permanency primarily influenced the date when breeding could begin at a site. At the road sites, anurans began breeding immediately at the start of the wet season. In contrast, although anurans were regularly observed and calling at sites off the road in the beginning of the wet season, they were unable to breed due to the lack of standing water.. When water accumulated at these sites, usually by July, activity increased sharply. Aichinger (1987) found that some species alter their breeding concentration from permanent to temporary sites as the wet season progressed. In the present study breeding activity did not decline at permanent sites as the temporary sites accumulated water, indicating that this movement did not occur.

Permanency can also act indirectly by influencing predation. The number of species vocalizing in the Savanna Site and Savanna lOOm Site was highest during the beginning of the rainy season each year. Most likely this pattern reflects species adaptation to an influx of fish causing increased predation later in the rainy season. Characteristic prolonged breeders at these sites seem to have adapted to a short breeding duration in response to fish predation on larvae.

Macrohabitat

The results reveal some vegetation characteristics that influence anuran community composition and structure at breeding pools in BNR. At the forest sites, canopy cover was typically closed and vegetation height was low. In contrast, the savanna sites had a more open canopy and higher vegetation growth. The road sites usually had intermediate levels and the Disturbed Site had low values for both vegetation characteristics. Comparisons of species richness and composition can be made with regard to savanna versus forest habitat sites and on-road versus off-road sites.

Sites in broadleaf forest habitat had higher species richness than the Savanna Site and Disturbed Site, with the exception of the Forest Site. Perhaps this can be explained by the greater predictability in climatic variables within forest habitat sites as reported by Inger and Colwell (1977). The forest sites had greater canopy cover than the savanna sites, resulting in less variability in daily temperature and relative humidity and consequently less stress on anuran species. Further evidence for increased stress in open canopy habitats can be found by examining species richness of the family Hylidae at different sites. Fifty percent of anurans at the Forest Entrance Site were hylids and 60% were hylids at the Forest Pool Site, whereas only 40% were hylids at the Savanna 100 m Site and Savanna Site and 43% at the Disturbed Site. Possibly the more variable environmental conditions in these habitats could explain this trend. Species present in the Savanna Site, Savanna 100 m Site, and Disturbed Site had to be tolerant of climatic extremes and able to adapt their lifestyles to minimize this stress. There was also less vertical microhabitat structure in savanna sites in comparison to forest sites, reducing the number of both perching and retreat locations. Therefore, terrestrial species that could exploit microhabitats within the vegetation or in burrows may have had an advantage over arboreal hylid species in these habitats.

In general, the road sites (Base of Hill Site, Forest Entrance Site, and Savanna 100 m Site) had higher species richness than off the road sites (Forest Site, Forest Pool Site, Transition Pool Site, and Savanna Site). The two forest road sites, Base of Hill Site and Forest Entrance Site, had 14 species each and the Savanna 100 m Site had a species richness of 10, equal to that of the Forest Pool Site and Transition Pool Site. It is important to remember that this data reflects the breeding site locations of these species. Many species encountered probably retreat to the uninterrupted habitat surrounding the road sites during the day and the dry season. However, the off-road breeding sites typically lacked some of the more common, habitat generalists such as *Bufo valliceps, Rana berlandieri, Hyla microcephala,* and *Smilisca bdudinii.* These habitat generalists primarily bred in small pools at sites along the road and were also commonly observed at the Disturbed Site. Meanwhile, habitat specialists bred with more frequency at sites off the road. For example, the Forest Pool Site did have high species richness (10) yet *B. valliceps* and *R. berlandieri* were never observed and evidence of breeding activity for *S. baudinii* was never found. Low species richness at the Forest Site was likely due to the inability of the pool to maintain water presence during the rainy season and at the Savanna Site it was probably due to fish predation.

The speciose road sites typically had intermediate levels of vegetation height and canopy cover in comparison to the off-road sites. In combination with high species richness, these traits indicate that the road sites acted as somewhat of an edge or disturbance in comparison to the surrounding habitat.. An increase in population density or species richness is associated with edge effects or transitional habitat (Gascon, 1993). Pearman (1997) found higher species richness at intermediate vegetation variables, with hylids seeming to benefit from anthropogenic disturbance involving a decrease in tree basal area, while species of *Eleutherodactylus* did not. Therefore, while total species richness may increase in areas of some disturbance, it is vital to analyze specific species responses to individual variables and their extremes. Forest habitat specialists such as *Hyla ebraccata* and *Gastrophryne elegans* did not avoid forest sites along the road, so it appears that these areas are not enough of a disturbance to influence more sensitive species. Yet the road sites may encourage the presence of disturbance tolerant species such as *Smilisca baudinii* and *Bufo valliceps* into areas they may otherwise not inhabit.

Habitat preferences

The results indicate that some species in the stUdy area ofBNR express distinct preferences to certain habitat characteristics. A range of habitat was examined during this study and overlap did exist for generalist species, yet sensitive species were encountered in specific preferred habitat.

Four species were described as breeding habitat generalists, i.e. utilizing each type of habitat surveyed in this study, *Rana berlandieri, Bufo valliceps, Smilisca baudinii, and Hyla microcephala.* One species *(Leptodactylus melanonotus)* specialized in sites across a range of canopy cover with low vegetation height. Nine species were considered to be breeding habitat specialists, either preferring forest sites with a closed canopy and little vegetation growth *(Agalychnis callidryas, Hyla loquax, Hyla ebraccata, Rhinophryas dorsalis,* and *Gastrophryne elegans)* or savanna sites with an open canopy and high vegetation growth (*Leptodactylus labialis, Hyla picta,* and *Scinax staufferi).* Breeding activity of *H picta* and S. *staufferi* was also regularly observed in transitional habitats.

In comparison to habitat generalists, specialists had a smaller range among the sites studied and were typically active during fewer months at lower calling indices, especially forest specialists. These trends indicate that specialist species had smaller population densities than the generalist species, a typical characteristic of specialists (Lawton, 1995). Since it is well known that habitat specialists are more sensitive to habitat change (Primack, 1993), these species may be more prone to experience declining populations. It is important for protected areas managers to understand the habitat preferences of specialists and incorporate them into management plans and decisions.

The Jaccard coefficient of similarity values reflect two patterns related to macrohabitat and site location. First, sites with greatet similarity in habitat characteristics, such as canopy cover, vegetation height, and vegetation type, also had a greater number of species in common. Forest sites matched with forest sites had higher Jaccard values than forest sites matched with savanna sites or the Disturbed Site. Second, the road sites had many species in common with each other, typically habitat generalists. Species such as *Leptodactylus labialis, Scinax staufferi,* and *Hyla picta* which were more typical of savanna sites, were also each encountered at the road sites in the forest, during one survey month. These observations may have inflated the Jaccard similarity values between the forest road sites and the Savanna 100 m Site.

Microhabitat

Inger and Colwell (1977) concluded that predictable environments have a more organized pattern of microhabitat overlap between species into guilds. Since species richness was greater in the more predictable forest habitats in this study, it follows that similar species should be partitioning the forest microhabitat to a greater degree. Resource partitioning can be illustrated by examining the key role vegetation plays in the spatial distribution of anurans. Species observed during this study can be characterized by their calling site microhabitat. . All except one of the hylids perched from locations above the ground on vegetation near to, or directly over, water.. *Smilisca baudinii,* the exception, would typically come to the ground and call at the edge of pools, although it was occasionally observed perching on vegetation. Perching locations and heights of hylid species were different, demonstrating vertical stratification. The bufonids, ranids, microhylid, and rhinophrynid would position themselves in water or at the edge of the water when calling. The leptodactylids seem to require vegetation or burrows for vocalizing. The greater variety of habitat within the forested sites allowed more species to co-occur within it by the use of different microhabitats, particularly in a vertical manner for perching hylid species.

Year-to- Year Comparisons of Species Activity and Abundance at Sites

The activity of some species was different in 2000 versus 2001 with regards to abundance, site locality, or breeding, but most species had a similar pattern each year of the study. Observed changes in activity may be due to the respective breeding strategy of the species, subtle changes in habitat or climatic variables at the sites, the days in which surveys were conducted, or an increase in species detection by the observer due to the learning curve.

Differences in year-to-year activity were especially noticeable for five species including *Hyla ebraccata, Gastrophryne elegans, Scinax staufferi, Hyla picta,* and

Leptodactylus labialis. Interestingly, all five of these species were characterized as breeding habitat specialists during the study. *Hyla ebraccata* called during three months in 2000 but only during one month in 2001. At first, this may seem to represent a decline in calling activity, but at anyone site the species only called during one or two months each year. Therefore this pattern probably reflects the short breeding duration of this species; however, *H ebraccata* also may have been encouraged to expend its breeding energy more rapidly in July 2001 by the abnormally low precipitation in June 2001.

Gastrophryne elegans called during May and July of2001 but was not heard in 2000. Since this species is an explosive breeder, its calling activity may have simply been missed during 2000. The other peculiarity of G. *elegans* was the high number of individuals found at the Base of Hill Site and Forest Entrance Site during April 2000, the only month in which this species was observed at these sites. As mentioned, this may have been a result of sediment disturbance or the extremely dry weather.

Hyla picta, Scinax staufferi, and *Leptodactylus labialis* were all characterized as breeding specialists of savanna habitat during this study, although *H picta* and S. *staufferi* also vocalized regularly in transitional habitat.. In addition, calling individuals of all three species were recorded at the Base of Hill Site and/or Forest Entrance Site during Mayor June surveys. More research is needed to determine whether these species actually breed in forest habitat ofBNR or if this data only represents a few individuals that traveled beyond their regular range. It is possible that *H picta* was heard calling more during 2001 due to an increase in the level of detection by the observer since this species has a relatively weak call that is difficult to detect when several species are calling together (Lee, 2000). Another interesting observation is that *H picta,* S. *staufferi,* and *1. labialis* were found during more months and in larger calling congregations at the Savanna 100 m Site and Savanna Site during 2001 in comparison to 2000. Most notably, *1. labialis* called during three months at both sites in 2000 but did not call at the Savanna Site and called only one month at index 1 at the Savanna 100 m site during 2001. Calling activity of the three species could have occurred during nights when surveys were not conducted, although this explanation is unlikely to explain the pattern reported for *1. labialis*. It is possible that fires in the savanna during April 2000 played a role in the population dynamics of these species. Fires have been found to increase pond productivity in the southeastern United States by releasing nutrients causing a parallel increase in the number of metamorphosing juveniles (Semlitsch, 2000).

Breeding activity, especially observations of amplexing individuals and eggs, was recorded with greater frequency during the 2001 wet season in comparison to 2000. It is possible that the 2001 survey days occurred during time periods better suited for anuran breeding, but more likely the observations were a result of increased detection by the observer and a greater accumulation of total field days. Likewise, additional species were observed at most sites during the 2001 wet season, raising the total species richness of each site. This is also probably a result of the accumulation of a greater number of total field days.

Summary

Spatial partitioning of anuran activity occurred by the use of different macro habitat and microhabitat within the study area. Activity at sites was highly dependent on water presence. Species demonstrated distinct breeding habitat preferences with some able to exist across the range of habitat and others specializing in either savanna or forest habitat. A few species had a different pattern of activity and abundance during 2000 than in 2001. Patterns in species abundance and community composition reflect physiological tolerances and species response to abiotic and biotic factors.

Future Direction

There are several limitations due to the methods used in this study and ways in which future work can be improved. Attaining twenty months of data is rare in tropical anuran community studies, yet it is still inadequate to obtain a reliable estimate of year-to-year trends in species abundance, as can be seen by the variation observed in this study. Obtaining additional years of data from these sites will help to understand the complexitites of anuran population dynamics in Belize. The statistical rigor of this study can be improved by increasing site replication. In this study, it was not possible to conduct multivariate statistical techniques that could make more conclusive statements regarding anuran habitat preference. In addition, it is important to keep in mind that the data presented were collected during a few days each month and the data on tadpole and metamorph life stages were not collected by formal methods. Therefore, results given are only a glimpse ofthe overall activity of the species and organization of the anuran communities. If surveys were conducted each day or week and if additional effort was focused on tadpole identification, a finer detail in the observed trends would likely become apparent. Finally, many more factors than studied may potentially play a role in the structuring of anuran communities and resource partitioning between species. The significance attached to certain biotic and abiotic variables examined in this study does not exclude the significance of other factors, such as competition and predation, and their role in structuring these communities.

Each of the items mentioned could be a direction for future research on anuran communities in southern Belize. If any of these recommendations were taken, the results would add to our understanding of anuran commmuntities.

Conclusions and management implications

Individual species partition the available resources in a habitat based on physiological and morphological tolerances as well as interspecies interactions such as predation and competition (Toft, 1985). Spatial and temporal resource partitioning results in the structure and composition of anuran communities. In this study, anuran community structure was influenced primarily by precipitation and macrohabitat..

On a tempQrallevel, breeding activity closely followed annual precipitation and water permanency at the sites. Breeding strategies differed by type (continuous vs. explosive), duration, and season. Spatial partitioning Of resources occurred on both macrohabitat and microhabitat levels, by use of different sites and vertical stratification. Species demonstrated preferences to habitat type and the forest habitat was more speciose than savanna habitat.. In addition, more species were characterized as specialists of forest habitat than of savanna habitat. Specialists of savanna habitat seemed to have greater tolerance for varying climatic and habitat conditions. For instance, the savanna habitat specialists were encountered on occasion in forest habitat, while the forest habitat specialists were never encountered in savanna habitat.. Specialist species also showed more variability in breeding activity from year to year than generalist species, which has important implications for future anuran population monitoring.

Patterns of species composition and richness relating to habitat variables were found in this study. This research indicates that it may be possible to predict areas where a species may occur based on factors such as canopy cover and vegetation height. Ultimately, it may be helpful to use such data to anticipate changes in anuran diversity due to habitat change, especially disturbance. Deforestation or fragmentation of lowland forests will alter pond hydroperiod and vegetation structure within a habitat. Newly fragmented areas are associated with changes in wind and sun exposure (Malcolm, 1994), which may result in changes in anuran species composition. In a similar manner, the succession of ponds and vegetation directly influences pond hydroperiod and canopy cover (Werner and Glennemeier, 1999); ponds examined with these changes had a great number of species extinctions over a 30-year period (Skelly et al., 1999). An increase or decrease in canopy cover will result in changes in abiotic factors such as temperature and humidity (Hubbell and Foster, 1986). Anurans, which are extremely sensitive to these abiotic factors, may be extirpated from areas where this change has occurred and/or the habitat may become more suitable for habitat generalists and opportunistic species. Certainly species respond differently to such changes, making it difficult to generalize about the effects of disturbance on anuran communities as a whole (Pearman, 1997; Marsh and Pearman, 1997). It is important to recognize changes in forest vegetation structure as forces that shape amphibian population dynamics. It is possible that changes in species composition will be found at the sites in this study due to the effects of Hurricane Iris, a Class IV hurricane, which devastated the canopy of the forest in the southwestern portion of BNR on 12 October 2001 (Meerman, 2001). The ability of specialist species to adapt to abrupt changes in vegetation structure at the forest sites will be tested by this natural disturbance event.

Temporal and spatial patterns in anuran activity are especially important to consider when planning monitoring programs for anurans. Larval success can change drastically from year to year based on pond hydroperiod, competition, and predation (Semlitsch, 2000) leading to fluctuating population sizes (Pechmann et al., 1991). Therefore, it would be easy to misinterpret results in anuran activity if the species are not well understood or if the data were collected during a brief time period. To minimize this issue, an essential first step when planning monitoring projects (Young et al., 2001) or the management of a protected area (Semlitsch, 2000) is to collect natural history information. It is also important to collect information on biotic and abiotic variables that may influence population dynamics. If well documented these variables may be used as indicators to estimate the future status of sensitive anuran populations, especially when extensive research can not be completed due to financial and time constraints (Pearman, 1997; Lips et al., 2001).

Understanding patterns in anuran activity, breeding and habitat preferences can help us to improve monitoring programs that identify population declines and to manage protected areas to preserve sensitive species. Habitat destruction is the greatest threat to amphibian populations and their conservation depends on maintaining effective biological reserves (Young, et al., 2001). Fortunately, Belize already has over 40% of its land under some level of protection. However, many of these protected areas currently lack a management plan and official presence. Village expansion, growth of shrimp and citrus industries, and unregulated use of pesticides and herbicides also pose threats to the future health of protected areas and the biota living in them. It is important that management plans be implemented and that they include a protocol for dealing with potential threats. The continuation of anuran monitoring programs will help to identify population declines early, hopefully in time to prevent a population crash. Yet, ultimately the fate of protected areas in Belize will depend on effective development and enforcement of regulations designed to preserve biodiversity.

LITERATURE CITED

Aichinger, M. 1987. Annual activity patterns of anurans in a seasonal neotropical environment. Oecologia 71:583-592.

Alford, R. A., and S. J. Richards. 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30:133-165.

Ankley, G. T., J. E. Tietge, D. 1. DeFoe, K. M. Jensen, G. W. Holcombe, E. 1. Durhan, and S. A. Diamond. 1998. Effects of ultraviolet light and methoprene on survival and development of *Rana pipiens.* Environmental Toxicology and Chemistry 17:2530-2542.

Beattie, R. C., and R. Tyler-Jones. 1992. The effects of low pH and aluminum on breeding success in the frog *Rana temporaria.* Journal of Herpetology 26:353-360.

Bertoluci, J. 1998. Annual patterns of breeding activity in Atlantic rainforest anurans. Journal ofHerpetology 32(4):607-611.

Blaustein, A. R., P. D. Hoffman, D. G. Hokit, J. M. Kiesecker, S. C. Walls, and J. B. Hays. 1994a. UV repair and resistance to solar UV-B in amphibian eggs: A link to population declines? Proceedings of the National Academy of Sciences of the United States of America 91: 1791-1795.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994b. Amphibian declines: Judging stability, persistence, and susceptibility of populations to local and global extinctions. Conservation Biology 8:60-71.

Blaustein, A. R., and D. B. Wake. 1995. The puzzle of declining amphibian populations. Scientific American 4:52-57.

Blaustein, A. R., P. D. Hoffman, J. M. Kiesecker, and J. B. Hays. 1996. DNA repair activity and resistance to solar UV-B radiation in eggs of the red-legged frog. Conservation Biology 10:1398-1402.

Brewer, S. W., and M. Rejmanek. 1999. Small rodents as significant dispersers of tree seeds in a neotropical forest. Journal ofVegeta!ion Science 10:165-174.

Campbell, 1. A. 1998. Amphibians and Reptiles of Northern Guatemala, the Yucatan, and Belize. University of Oklahoma Press, Norman, USA.

Campbell, J. A. 1999. Distribution patterns of amphibians in Middle America. *In* W. E. Duellman (ed.), Patterns of Distribution of Amphibians: A Global Perspective, pp. 111-210. John Hopkins University Press, Baltimore, MD, USA.

Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. *In* M. L. Cody and J. Diamond (eds.), Ecology and Evolution of Communities, pp. 460-490. Harvard University Press, Cambridge, MA.

Conservation International. 1990. The Rain Forest Imperative. Conservation International, Washington, D. C., USA.

Creusere, F. M., and W. G. Whitford. 1976. Ecological relationships in a desert anuran community. Herpetologica 32:7-18.

Crump, M. L. 1971. Quantitative analysis of the ecological distribution of a tropical herpetofauna. Occasional Papers of the Museum of Natural History, University of Kansas 3: 1-62.

Crump, M. L. and N. J. Scott, Jr. 1994. Visual encounter surveys. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, pp. 84-92. Smithsonian Institution Press, Washington, D. C., USA.

Crump, M. L., F. R. Hensley, and K. L. Clark. 1992. Apparent decline of the golden toad: Underground or extinct? Copeia 1992:413-420.

Donnelly, M. A., and C. Guyer. 1994. Patterns of reproduction and habitat use in an assemblage ofNeotropical hylid frogs. Oecologia 98:291-302.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. Miscellaneous Publication of the University of Kansas Museum of Natural History 65: 1-352.

Duellman, W. E. 1999. Global distribution of amphibians: patterns, conservation, and future challenges. *In* W. E. Duellman (ed.), Patterns of Distribution of Amphibians: A Global Perspective, pp. 1-30. John Hopkins University Press, Baltimore, MD, USA.

Duellman, W. E., and L. Trueb. 1994. Biology of Amphibians. The John Hopkins University Press, Baltimore, MD, USA and London, England.

Dunson, W.A., and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist 138:1067-1091.

Eterovick, P. C., and I. Sazima. 2000. Structure of an anuran community in a montane meadow in southeastern Brazil: effects of seasonality, habitat, and predation. Amphibia-Reptilia 21:439-461.

Gardner, T., M. Bol, F. Bucknill, N. Coc, E. Fitzherbert, and N. Hart. 2001. An ecological research project concerned with the assessment and monitoring of anuran populations in the region around Las Cuevas, Chiquibul Forest Reserve, Belize Phase II: Preliminary Report. Unpublished report.

Gascon, C. 1991. Population- and community-level analyses of species occurrences of central Amazonian rainforest tadpoles. Ecology 72(5):1731-1746.

Gascon, C. 1993. Breeding-habitat use by five Amazonian frogs at forest edge. Biodiversity and Conservation 2:438-444.

Hecnar, S. J. 1995. Acute and chronic toxicity of arnmonuim nitrate fertilizer to amphibians from southern Ontario. Environmental Toxicology and Chemistry. 14:2131-2137.

Heyer, W. R., R. W. McDiarmid, and D. 1. Weigman. 1975. Tadpoles, predation, and pond habitats in the tropics. Biotropica 7:100-111.

Houlahan, J. E., C. S. Findlay, B. R. Schidt, A. H. Meyer, and S. 1. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. Nature 404:752-755.

Hubbell' S. P., and R. B. Foster.. 1986. Canopy gaps and the dynamics of a neotropical forest.. *In* M. J. Crawley (ed.), r;>lantEcology, pp. 77-95. Blackwell Scientific, Oxford, England.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology 22:415-427.

Inger, R. F., and R. K. Colwell. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecological Monographs 47:229-253.

Kiesecker, J. M., and A. R. Blaustein.1997:-fnfluences of egg laying behavior on pathogenic infection of amphibian eggs. Conservation Biology 11:214-220.

Krebs, C. J. 1999. Ecological Methodology, 2nd edition. Addison-Welsey Educational Publishers, Inc., Menlo Park, CA, USA..

Lannoo, M. J., K. Lang, T. Waltz, and G. S. Phillips. 1994. An altered amphibian assemblage: Dickinson County, Iowa,'70 years after Frank Blanchard's Survey. The American Midland Naturalist 131:311-319.

Laurance, W. F. 1996. Catastophic declines of Australian rainforest frogs: Is unusual weather responsible? Biological Conservation 77:203-212.

Laurance, W. F., K. R. McDonald, and R. Speare. 1996. Epidemic disease and the catastrophic decline of Australian rain forest frogs. Conservation Biology 10:406-413.

Lawton, J. H. 1995. Population dynamic principles. *In* J. H. Lawton and R. M. May (eds.), Extinction Rates, pp. 147-163. Oxford University Press, New York, USA..

Lawton, J. H. 1999. Are there general laws in ecology? Oikos 84:177-192.

Lee, J. C. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World. Cornell University Press, Ithaca, NY, USA..

Lips, K. R., J. K. Reaser, B. E. Young, and R. Ibanez. 2001. Amphibian monitoring in Latin America: a protocol manual.. Herpetological Circulars 20: 1-115.

Malcolm, J. R. 1994. Edge effects in central Amazonian forest fragments. Ecology 75:2438-2445.

Marsh, D. M., and P. B. Pearman.. 1997. Effects of habitat fragmentation on the abundance of two species of leptodactylid frogs in an Andean montane forest.. Conservation Biology 11:1323-1328.

McNaughton, S. J., and L. L. Wolf. 1979. General Ecology, 2nd edition. Holt, Rinehart, and Winston. New York, USA..

Meerman, J. C. 2001. A first assessment of damage to terrestrial ecosystems in southern Belize as caused by Hurricane Iris of October 8, 2001. Belize Environmental Consultancies Ltd., Belize. Unpublished report

Meerman, J. C., and W. Sabido. 2001. Central American ecosystems map: Belize. Volume I and II. Programme for Belize. Unpublished report.

Meyer, J. R. 1997. MAYAMON-Maya Forest Anuran Monitoring Project-General information for participants. Unpublished report.

Meyer, J. R., and C. F. Foster.. 1996. A Guide to the Frogs and Toads of Belize. Krieger Publishing Company, Malabar, FL, USA.

Ouellet, M., J. Bonin, J. Rodrigue, J. DesGranges, and S. Lair. 1997. Hindlimb deformities (ectromelia, ectrodactyly) in free-living anurans from agricultural habitats. Journal of Wildlife Diseases 33:95-104.

Pearman, P. B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador.. Conservation Biology 11:1211-1225.

Pearman, P. B., A. M. Velasco, and A. Lopez. 1995. Tropical amphibian monitoring: A comparison of methods for detecting inter-site variation in species' composition. Herpetologica 51:325-335.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3-11.

Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. 1. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: The problem of separating human impacts from natural fluctuations. Science 253:892-895.

Phillips, K. 1990. Where have all the frogs and toads gone? Bioscience 40:422-424.

Pough, F. H., R. M. Andrews, J. E. Cadle, M. L. Crump, A. H. Savitzky, and K. D. Wells. 1998. Herpetology. Prentice Hall, Upper Saddle River, NJ, USA.

Pounds, J. A., and M. L. Crump. 1994. Amphibian declines and climate disturbance: the case of the golden toad and the harlequin frog. Conservation Biology 8:72-85.

Primack, R. B. 1993. Essentials of Conservation Biology. Sinauer Associates, Inc., Sunderland, MA, USA..

Prince, P. 1984. Communities of specialists: Vacant niches in ecological and evolutionary time. *In* Strong, D.R., D. Simberloff, L. G. Abele, and A. B. Thistle (eds.), Ecological Communities, Conceptual Issues and the Evidence, pp. 510-523. Princeton University Press, Princeton, NJ, USA.

Rand, A. S., and C. W. Myers. 1990. The herpetofauna ofBarro Island, Panama: an ecological summary. *In* Gentry, A. H. (ed.), Four Neotropical Rainforests, pp. 386-409. Vail-Ballou Press, Binghamton, NY, USA.

Sadinski, W. 1., and W. A. Dunson. 1992. A multilevel study of effects of low pH on amphibians of temporary ponds. Journal of Herpetol6gy 26:413-422.

Sarkar, S. 1996. Ecological theory and anuran declines. Bioscience 46:199-207.

Scott, N. J. Jr., Savage J. M., Robinson, D. C. 1983. Checklist of reptiles and amphibians. *In* Janzen, D. H. (ed.), Costa Rican Natural History, pp. 367-374. University of Chicago Press, Chicago, I-L,USA.

Semlitsch, R. D. 2000. Principals for management of aquatic-breeding amphibians. Journal of Wildlife Management 64:615-631..

Shirose, L. J., C. A. Bishop, D. M. Green, C. J. MacDonald, R. J. Brooks, and N. J. Helferty. 1997. Validation tests of an amphibian call count survey technique in Ontario, Canada. Herpetologica 53(5):312-320.

SkellY' D. K. E. E. Werner, and S. A. Cortwright.. 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80(7):2326-2337.

Stewart, M. M. 1995. Climate driven population fluctuations in rain forest frogs. Journal of Herpetology ·29:437-446.

Strijbosch, H. 1980. Habitat selection by amphibians during their terrestrial phase. British Journal of Herpetology 6:93-98.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Tyler, T., W. J. Liss, L. M. Ganio, G. L. Larson, R. Hoffman, E. Deimling, and G. Lomicky. 1998. Interaction between introduced trout and larval salamanders *(Ambystoma macrodactylum)* in high-elevation lakes. Conservation Biology 12:94-105.

Vonesh, J. R. 2001. Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. Biotropica 33(3):502-510.

Welborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient.. Annual Review of Ecology and Systematics 27:337-363.

Wells, K. D. 1977. The social behavior of anuran amphibians. Animal Behaviour 25:666-693.

Werner, E. E., and K. S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999(1): 1-12.

Whitmore, T. C. 1990. An Introduction to Tropical Rain Forests. Oxford University Press, New York, USA..

Wild, E. R. 1996. Natural history and resource use of four Amazonian tadpole assemblages. Occasional Papers of the Natural History Museum, The University of Kansas 176:1-59.

Williams, S. E., and J. Hero. 1998. Rainforest frogs of the Australian wet tropics: Guild classification and the ecological similarity of declining species. Proceedings of the Royal Society of London Biological Sciences 265:597-602.

Young, B. E., K. R. Lips, J. K. Reaser, R. Ibanez, A. W. Salas, J. R. Cedeno, L. A. Coloma, S. Ron, E. La Marca, J. R. Meyer, A. Munoz, F. Bolanos, G. Chaves, and D. Romo. 2001. Population declines and priorities for amphibian conservation in Latin America. Conservation Biology 15:1213-1223.

Zar, J. H. 1996. Biostatistical Analysis, 3rd edition. Prentice Hall, Upper Saddle River, NJ, USA.

Zimmerman, B. L. 1994. Audio strip transects. *In* W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians, pp. 92-97. Smithsonian Institution Press, Washington, D. C., USA.

Appendix 1. Calling indices and number of individuals observed[a] of each species at the Bladen River Crossing Site from 2000-2001.

	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus	1	2*(7)	1+(5)	(1)	(1)	2(1)	1(1)	1+(1)	1+(1)	2+(3)		2(3)	2(1)		2(2)		(2)	1(1)	1-(3)	2*(3)	1+(2)
Bufo valliceps			(1)		(1)	(2)										2(7)		3*(10)	1-		-
Agalychnis callidryas																					
Hyla ebraccata																					
Hylaloquax																					
Hyla microcephala																					
Hylapicta																					
Scinax staufferi				1																	
Smilisca baudinii											+(1)	+									
Smilisca cyanosticta																					
Gastrophryne elegans																					
Rana berlandieri		(1)								(1)		(1)				(1)					*(6)
Rana vaillanti		(2)	(1)			(1)				(1)	(1)	(2)	(1)		(1)	(1)	(1)	(1)			
Leptodactylus labialis																					
Leptodactylus melanonotus																					
Rhinophryas dorsalis																					
Total # observed/ calling	0/1	3/1	3/1	1/1	2/0	3/1	1/1	1/1	1/1	3/1	2/0	3/1	2/1		2/1	3/1	2/0	3/2	1/2	1/1	2/1

Notes: a = Highest number calling or observed (in parentheses) during anyone survey each month

I = 1-5 individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.

* = amplexus or eggs observed, + = tadpoles or metamorphs observed

- = possible breeding evidence but not confirmed

No surveys were conducted in March 2001.

Appendix 2. Calling indices and number of individuals observed[a] of each species at the Base of Hill Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug.	Sept	Oct
Bufo marinus				(1)		(1)										(1)	(l)				
Bufo valliceps			(2)	(4)	(1)		4*(13)			(1)						(1)	*+(4)	+(1)			-
Agalychnis callidryas					1	1(2)	2(1)	2								1	2*(4)	2*	1*	1	
Hyla ebraccata			(1)															1			
Hyla loquax							2											2*(8)		1	
Hyla microcephala			(3)		(1)	1	2(4)	2(2)								2(3)	2(1)	2-(5)	2(2)	1(1)	
Hylapicta																2					
Scinax staufferi																					
Smilisca baudinii			(2)	(1)	*(3)	1(1)	3*+(8)	2(1)									4*+(13)	+	*+	(1)	-
Smilisca cyanosticta																					
Gastrophryne elegans			(10)																		
Rana berlandieri			(1)		(1)	(1)	(4)	+	(2)	+(3)	(2).	(3)				-(1)	-(~)	1*(2)			
Rana vaillanti			(2)		(1)	(1)		+(1)	(1)	+(6)	(2)	(1)	(1)			(1)	-(1)	(1)			(2)
Leptodactylus labialis			(1)														1				
Leptodactylus melanonotus			(1)								(1)										
Rhinophryas dorsalis																1(2)					
Total # observed/calling			9/0	3/0	5/1	5/3	5/5	3/3	2/0	3/0	3/0	2/0	1/0		0/0	6/4	7/4	5/5	1/2	2/3	1/0

Notes: a = Highest number calling or observed (in parentheses) during anyone survey each month

I = 1-5individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.

* = amplexus or eggs observed, + = tadpoles or metamorphs observed

\- = possible breeding evidence but not confirmed

Surveys began in the site in April 2000 and no survey was conducted in March 2001.

Appendix 3. Calling indices and number of individuals observed[3] of each species at Forest Entrance Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus				(2)	(1)											(3)	(1)		(1)		
Bufo valliceps				(2)	+(1)		+									3*+(44)	3(5)		(1)		
Agalychnis callidryas				1	2(2)	2(1)	2(1)	2	1							2*(2)	2(1)	2*(2)	2	1	
Hyla ebraccata								1(1)										1(1)			
Hyla loquax						1(1)	2+(1)	1	+									2-(1)	1	1	
Hyla microcephala				1(2)	2(4)	4*(2)	2-(1)	1	+							4*(12)	3(8)	3*(8)	2(3)	1(1)	
Hylapicta																2(1)					
Scinax staufferi																1					
Smilisca baudinii		(2)		2(2)	2(2)	1	(1)	(1)	(1)	+					(1)	1*+(1)	4*(45)		1*(1)		-
Smilisca cyanosticta																					
Gastrophryne elegans			(17)																		
Rana berlandieri				(1)	(2)	-	1*(8)	2-(2)	(1)	+(1)			(1)			2*(6)	1*(3)	2*(3)		-	
Rana vaillanti		(1)			(3)	-		-(1)	+	+(1)	(1)	(2)	(1)			(1)	(4)	(1)	(1)	-	(1)
Leptodactylus labialis																					
Leptodactylus melanonotus					1(1)	1									(4)-			1		1	
Rhinophryas dorsalis				3*+(14)	+											1+(1)					
Total # observed/calling		2/0	1/0	6/4	8/4	3/5	5/4	4/5	2/1	2/0	1/0	1/0	2/0		2/0	9/8	7/5	6/6	5/4	1/4	1/0

Notes: 3 = Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20,3 = 21-50, and 4 = >50.

* = breeding evidence (amplexus, eggs, tadpoles or metamorphs observed)

- = possible breeding evidence but not confirmed

Surveys began in March 2000 and no survey was conducted in March 2001.

Appendix 4. Calling indices and number of individuals observed[a] of each species at the Forest Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dee	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oet
Bufo marinus																					
Bufo valliceps	(1)		(1)	(2)	+(2)	(1)		(3)	(3)	(1)								(1)			
Agalychnis callidryas				1	1																
Hyla ebraccata																					
Hyla loquax																					
Hyla microcephala																					
Hyla picta				2(1)																	
Scinax staufferi																					
Smilisca baudinii					(1)				(1)	(2)						2*(5)					
Smilisca cyanosticta																					
Gastrophryne elegans							+(2)														
Rana berlandieri																					
Rana vaillanti																					
Leptodactylus labialis																					
Leptodactylus melanonotus																					
Rhinophryas dorsalis																					
Total # observed/calling	1/0	0/0	1/0	2/2	2/1	1/0	1/0	1/0	2/0	2/0	0/0	0/0	0/0			1/1	0/0	1/0			0/0

Notes: a = Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.

* = amplexus or eggs observed, + = tadpoles or metamorphs observed

- = possible breeding evidence but not conftrmed

No surveys were conducted in the site during March, April, August, or September, 2001..

Appendix 5. Calling indices and number of individuals observed[a] of each species at the Forest Pool Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus																					
Bufo valliceps																					
Aga/ychnis callidryas						4*(5)	3(3)	2(1)	1	1						1		3(1)	1	1*	1-
Hy/a ebraccata						2(1)	2-											2			
Hy/a /oquax						2(1)	2	2										2		1	
Hy/a microcepha/a						4(5)	3(1)	2(1)								1		4*(15)	3-	1	2
Hy/apicta																					
Scinax staufferi																1					
Smilisca baudinii																	(I)				
Smilisca cyanosticta																					
Gastrophryne e/egans																		+	+	+	
Rana berlandieri																					
Rana vaillanti						(2)	(4)	(2)	-(I)	(1)								(3)	(I)	(1)	
Leptodacty/us /abialis																					
Leptodacty/us me/anonotus					2	2(1)	2	1												1	1
Rhinophryas dorsalis																		+	+		
Total # observed/calling					all	5/6	3/5	3/4	1/1	1/1	0/0	0/0	0/0			0/3	1/0	3/4	1/2	1/4	0/3

Notes: [a] = Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20,3 = 21-50, and 4 = >50.

* = breeding evidence (amplexus, eggs, tadpoles or metamorphs observed)

- = possible breeding evidence but not conftrmed

Surveys began in the site in June 2000 and no surveys were conducted during March or April 200 1.

Appendix 6. Calling indices and number of individuals observed[8] of each species at the Transition Pool Site from 2000-2001..

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oet	Nov	Dee	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oet
Bufo marinus																					
Bufo va/liceps							1(2)									(1)	-(1)				-
Agalychnis callidryas						2	1	2								1	1	2*(2)	2	1	
Hyla ebraccata																					
Hyla loquax																					
Hyla microcephala					3	4	2(1)	2								1		4(11)	2	1-	
Hylapicta						1(1)	2(1)	1										1(1)	1	1-	
Scinax staufferi						2(2)	1									1		2			
Smilisca baudinii										-							+	+(1)	*(1)		-
Smilisca cyanosticta																					
Gastrophryne elegans																		1			
Rana berlandieri								(1)	(1)	-								-(2)			-
Rana vaillanti									(1)	-(1)	(1)	(1)						-(1)			-
Leptodactylus labialis																					
Leptodactylus melanonotus						2	1											1	1	-(1)	
Rhinophryas dorsalis																					
Total # observed/calling					0/1	2/5	3/6	1/3	2/0	1/0	1/0	1/0	0/0			1/3	1/1	6/6	1/4	1/3	0/0

Notes: a = Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20,3 = 21-50, and 4 = >50.

* = ~mp1exus or eggs observed, + = tadpoles or metamorphs observed

- = possible breeding evidence but not confIrmed

Surveys began in the site in June 2000 and no surveys were conducted in March or April 2001.

Appendix 8. Calling indices and number of individuals observed[a] of each species at Savanna Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus																					
Bufo valliceps						(1)															
Agalychnis callidryas																					
Hyla ebraccata																					
Hyla loquax																					
Hyla microcephala					2											2		1			
Hylapicta																					
Scinax staufferi			(1)	2(1)	2	3(3)	4(1)	1								1		3(1)	1		
Smilisca baudinii																					
Smilisca cyanosticta																					
Gastrophryne elegans																					
Rana berlandieri						1*		-(1)	(2)							-		-			
Rana vaillanti								-								-		-			
Leptodactylus labialis				4(1)	4(2)	2	+	+	(1)			(1)									
Leptodactylus melanonotus																					
Rhinophryas dorsalis																					
Total # observed/calling	0/0	0/0	1/0	2/2	1/3	2/3	1/1	1/1	2/0	0/0	0/0	1/0	0/0			0/2	0/0	1/2	0/1		0/0

Notes: a = Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.

* = amplexus or eggs observed, + = tadpoles or metamorphs observed

- = possible breeding evidence but not conflrmed

No surveys were conducted during March, April, or September 2001.

Appendix 9. Calling indices and number of individuals observed· of each species at the Disturbed Site from 2000-2001.

Species Name	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct
Bufo marinus																1(3)					
Bufo valliceps																3(2)					
Agalychnis callidryas																					
Hyla ebraccata																					
Hyla loquax																					
Hyla microcephala							4(5)									2(2)			1(1)		
Hylapicta																					
Scinax staufferi							4(6)									1			2		
Smilisca baudinii							2(3)									3			1		
Smilisca cyanosticta																					
Gastrophryne elegans																					
Rana berlandieri																(1)					
Rana vaillanti																					
Leptodactylus labialis																					
Leptodactylus melanonotus							1												2		
Rhinophryas dorsalis																					
Total # observed/calling				0/0			3/4			0/0						4/5			1/4		

Notes: ·=Highest number calling or observed (in parentheses) during anyone survey each month

1 = 1-5 individuals calling, 2 = 6-20, 3 = 21-50, and 4 = >50.

* = amplexus or eggs observed, + = tadpoles or metamorphs observed

- = possible breeding evidence but not confirmed

Surveys were only conducted during the five months data is presented for.