



**Project Anuran Phase I:
Main Report**

**An ecological research project concerned with
the assessment and monitoring of anuran
populations in the region around Las Cuevas,
Chiquibul Forest Reserve, Belize.**

BY

**Toby Gardner, Emily Fitzherbert, Nick Hill
and Lorry Williams**

June 2001

Project Anuran
Institute of Ecology and Resource Management
University of Edinburgh
Darwin Building
Kings Buildings
Mayfield Road
EH9 3JU
Edinburgh, Scotland
Email: ProjectAnuran@hotmail.com
Website: www.projectanuran.org

Summary

In the last 20 years the scientific community has become increasingly concerned following a growing number of reports documenting global amphibian declines. Observations of frequently catastrophic amphibian declines in areas of the world previously thought to be undisturbed by man, has led to the suggestion that human-induced global agents are responsible for declines. The fact that amphibians play in an integral role in the functioning of many ecosystems, points to the potentially drastic consequences of large-scale population declines. Furthermore, due to their bi-phasic lifestyle, existing in both aquatic and terrestrial habitats, coupled with their highly permeable skin, they can act as excellent indicators of environmental health – a fact that bears worrying implications for humans in light of their increasing demise. In order to resolve the phenomenon of declining amphibian populations, and consequently take appropriate conservation action, there is a desperate need for long-term and intensive monitoring programs. The aim of Project Anuran is to undertake a comprehensive monitoring program of an entire community of amphibians across a suite of study sites, in the region of the neotropical research station at Las Cuevas, Belize. Using standard protocols of vocalisation surveys, and nocturnal visual searches detailed data was collected during summer 2000 on the diversity, relative abundance, and habitat associations of local amphibian populations. This data serves to provide an excellent baseline against which future population assessments can be compared. Detailed surveillance of the temporal patterns of reproductive activity provided an insight into the temporal partitioning of peak vocalisation activity – an insight which is vital in gaining an understanding of the pattern, organisation and underlying mechanisms which structure amphibian communities. Due to limitations of time, expertise, and money, comprehensive ecological assessments of amphibian communities are rare throughout most of the neotropics. It is felt that undergraduate projects such as Project Anuran, in liasing with the student communities of such countries, are ideally placed to provide the necessary man power, resources, and enthusiasm, required to produce the desperately needed data from comprehensive monitoring programs.

Contents

Chapter	Pages
Acknowledgements	5
Chapter 1: Background and Justification	
The declining amphibian phenomenon	6-7
The importance of amphibians in ecological and human environments	7-8
Evidence for global amphibian declines	8-11
Candidates for amphibian decline	11-20
Monitoring of amphibian populations: points to note	20-23
Chapter 2: Role of Project Anuran	24-25
Chapter 3: Aims and Objectives	26
Chapter 4: Methodology and Approach	27-32
Chapter 5: Results	
Overview	33
Weather	34
Field Study 1: Vocalising Species	35-38
Individual Species Accounts	39-53
Individual Site Accounts	54-70
Analysis of Community Structure	70-75
Field Study 2: Non-vocalising and leaf litter species	75-77
Chapter 6: Discussion	78-84
References	85-93
Appendices	
Appendix 1: Site Map	94
Appendix 3: Pond Maps	95-100
Appendix 4: Raw Data Tables	102-114
Appendix 5: Treasury Report	116

Acknowledgements

This project could never have moved beyond conception if it was not for a huge amount of help and support from a great number of people. The members of the project are extremely grateful to the very generous support of the following benevolent, organizations, trust funds, companies and individuals. If it was not for the existence of such bodies, this project (nor any other) could never have become a reality. To you all we are indebted: **Alumni & Development Trust (UoE), Barnson Bequest (UoE), British Ecological Society, Davis Expedition Trust (UoE), Edinburgh Trust No. 2, Gilchrist Educational Trust, James Rennie Bequest (UoE), Life Support Training Services, Mr & Mrs Lean , Mrs Fitzherbert-Brockles, Royal Geographic Society, Royal Scottish Geographic Society, Royal Scottish Zoological Society, Tiso, Trips Worldwide, Weir Fund for Field Studies (UoE).**

A great number of individuals have been instrumental in the development and success of this project. Our achievements are greatly attributable to the immense support and encouragement that we found wherever advice was sought. Thanks go to all the staff and speakers of the RGS Explore 99 for giving us the initial idea and encouragement. A great number of people have gone beyond their call of duty to offer advice and support, particular thanks goes to Daryl White and the staff of LSTS, Mr John Anthony and the staff of the photography lab in the Darwin Building, Dr Sutton and Dr Knapp of the museum, Professor John Grace, Dr Graham Russell and Mrs Margaret Jackson, of the University of Edinburgh. We are especially indebted to Dr Peter Stafford of the Natural History Museum, Professor Julian Lee of the University of Miami, and John Wilkinson and Dr Jack Meyer of the DAPTF for their considerable advice on herpetological matters and their kind patience in the face of ceaseless emails and pleas for help. Professor Peter Furley of the University of Edinburgh gave unstinting support throughout the development and execution of the project, to him we are especially grateful. Our time in Belize was made immensely enjoyable and rewarding thanks to the considerable efforts of the staff of the research station; Mr Chris Minty, Mr Nicodemus Bol, Mrs Celia Bol and Mr Enrique Saquil. To all the above and countless more unnamed people, thank you.

The declining amphibian phenomenon

Human alteration of the global environment namely through habitat modification, agricultural practices, anthropogenically induced climate change, and atmospheric pollutants has triggered what is widely regarded as the sixth major extinction event in the history of life (Chapin *et al.* 2000). The extent of loss of biological diversity, and alterations in the distribution of organisms shows considerable variance both with respect to geographic location but also with respect to the ecological and taxonomic characteristics of the species involved. Usually proximal factors such as habitat destruction or modification are easily identified as the responsible cause of local losses of biodiversity, and as such local reductions in biodiversity are most frequently observed across the taxonomic spectrum. It is therefore with particular alarm that biologists are reporting a rapidly mounting picture of dwindling populations and extinctions from across the six continents of the earth, often in areas previously thought to be intact from human disturbance, of specifically one major taxonomic group – that of amphibians. The suspicion that amphibians are suffering from an unprecedented and abnormally high rate of decline was first voiced at the First World Herpetology Conference in September of 1989, in Canterbury, England (Barinaga 1990), although it is clear that widespread concern existed long before this (Bury 1999). The seriousness with which the scientific community recognised this problem was reflected in the rapid organisation of a NRC sponsored workshop in February of 1990, in Irvine USA, and in light of the perturbing reports presented (Blaustein & Wake 1990; Wake 1991), the establishment of a special task force on declining amphibian populations (DAPTF), allied with the Species Survival Commission of the IUCN. During the subsequent decade neither the scale of the problem nor the widespread concern expressed in both the scientific (Wake 1998), and public (Blaustein & Wake 1995; Morell 2001) community has seen any abatement. In order to tackle any problem in ecology it is essential that one is aware of the present level of understanding of its scale, diagnostic characteristics, and methodologies appropriate to its resolution. We feel that to lack such appreciation is unjustified, especially in consideration of the important consequences of amphibian declines, and furthermore could lead to inefficient, repetitive, or even counterproductive research. This background section to our own work hopes to go some way to providing such an appreciation, with particular reference to our study area of Belize, and deals in turn with; (1) the ecological and human importance of amphibians in natural ecosystems, (2) evidence for population declines and caveats in their interpretation, (3) the range of

candidates which have been proposed to explain such declines, and (4) the present challenge facing ecologists and the role of Project Anuran in helping to meet it.

The importance of amphibians in ecological and human environments

A world-wide decline of amphibians could have a significant and detrimental impact on both other organisms and humans. Amphibians are integral components of many ecosystems, often constituting the highest fraction of vertebrate biomass (Burton & Likens 1975; Beebee 1996). Their conspicuous role is noted to be of particular importance in tropical forests where, in acting as both predator and prey species, they play a key role in trophic dynamics (Toft 1980a; Blaustein *et al.* 1994a). Their high collective biomass, alongside their high digestion and production efficiencies (Woolbright 1991) go some way to explaining their potential importance in such ‘functions’ as the maintenance ecosystem energetics and carbon flow (Pearman 1997) – namely through the maintenance of arthropod abundance (Guyer 1990), and the provision of an critical prey base for higher order predators, such as arachnids, snakes, and birds (Guyer 1990; Woolbright 1991; Duellman & Trueb 1994). In identifying the functional significance of amphibians it is clearly of relevance to understand whether the species diversity per se plays a unique role over and above species *identity* – i.e. are a few specific and perhaps more abundant frog species sufficient to maintain the natural integrity and productivity of the ecosystem? This question is particularly prevalent in the case of neotropical forests, which hosts the world’s highest amphibian diversity, including the most diverse of all vertebrate genera – the leaf frogs, *Eleutherodactylus* (Lee 1996). In view of the limitations on the world’s resources for the conservation of biodiversity, it would seem sensible to identify the functionally important amphibian species or ‘guilds’ in order to prioritise concern and subsequent potential conservation action following a reported decline in number. However such an approach could be very dangerous, as it is often extremely difficult if not impossible to identify the functional role or contribution of many species (Chapin *et al.* 2000). Although some (limited) empirical evidence exists to offer an explicit justification for the functional importance of biodiversity per se (e.g. Naeem *et al.* 1994; Tilman *et al.* 1996, Jonsson & Malmquist 2000), a perhaps more convincing argument is that although many species may be presently largely redundant in function, they could play a crucial role in filling a shift in niche space following extinctions of other species or climate change (Loreau 2000). In light of our ignorance of the ecology of most amphibians (Alford &

Richards 1999), and growing evidence of global climatic change, it seems that an attitude of concern towards all populations that could be potentially at risk is prudent, if not essential.

The second most recognised importance of amphibians is their potential role as indicators of global environmental health and resilience (Blaustein & Wake 1990; Barinaga 1990; Diamond 1996). They inhabit both aquatic and terrestrial habitats, and are thus exposed to aquatic and terrestrial pollutants – to which they are particularly sensitive due to their highly permeable skin (Duellman & Trueb 1994). Furthermore they are ‘exposed’ to a large extent of the biotic environment, due to their roles as both herbivores during larval stages and carnivores as adults, making them potentially good indicators of changes in both floristic and faunal community composition – possibly induced through environmental stress. As Barainaga (1990) states, the fact that amphibians as a group have remained largely unchanged since the era of the dinosaurs, highlights the potentially disastrous consequences for humans and other species if their suspected demise continues unabated. Finally, from a purely human perspective amphibians represent a storehouse of pharmaceutical products waiting to be exploited fully (Blaustein & Wake 1995). Some compounds already extracted are presently being used as painkillers and in the treatment of traumas such as burns and heart attacks, whilst many more undoubtedly await discovery.

Evidence for global amphibian declines

Although serious recognition of the potential problem of declining amphibians was not afforded until the last decade, individual anecdotal reports of population declines have been known in America since the late 18th century (Bury 1999). However it was during the 1980’s and early 1990’s that the observations of more dramatic and scientifically credible declines were made. Such declines include notable individual examples such as the Golden toad (*Bufo periglenes*) and Harlequin frog (*Atelopus varius*) (Crump *et al.* 1992; Pounds & Crump 1994), the Cascades frog (*Rana cascade*) (Fellers & Drost 1993), and the Yellow and Red-legged frogs (*Rana muscosa* and *Rana aurora*) (Blaustein & Wake 1990). All of these declines have occurred in areas considered largely intact from human interference, which explains their common citation in justifying concern for the viability of other seemingly well protected amphibian populations. Further evidence for the apparent vulnerability of the class Amphibia as a whole comes from reports of population declines across whole communities of amphibians at the regional level, and also in relatively pristine areas; the Atlantic forests of Brazil

(Heyer *et al.* 1988), the Central Valley of California (Drost & Fellers 1996, Fisher & Shaffer 1996), the montane forests of Eastern Australia (Laurance *et al.* 1996), and the Monteverde cloud forest of Costa Rica (Lips 1998, 1999). It is hard to draw global conclusions from such varied examples, although two salient points are clear (Lips 1998; Alford & Richards 1999); (1) there is significant interspecific variation in population vulnerability, with many species sympatric to the above declining population examples appearing to maintain their stability, and (2) there is significant geographic variation with respect to the focus of declines, with the most rapid declines appearing in North West USA, Central America, and Australia. However, such variation is perhaps far more an artificial product of the distribution of amphibian biologists and research institutes, than the product of actual variation in ecological conditions or species attributes. To remove some of this bias and view the declining amphibian problem from a more global perspective, it is necessary to collate information from across many sites and many species.

In attempting to draw global conclusions or patterns about a particular ecological phenomenon (such as population declines) from across different studies, one is commonly faced with two main problems; the inaccessibility of many research reports, and the extreme variability in monitoring techniques used – from the purely anecdotal to the scientifically rigorous. A number of recent reviews have attempted such a difficult collaboration in order to view the plight of amphibians from the widest possible perspective – both at spatial and temporal scales, the two most noteworthy of which are those of Alford & Richards (1999) and Houlahan *et al.* (2000). Alford & Richards (1999) considered 85 time series of amphibian populations spanning the period between 1951-1997, and following regression analysis concluded that more populations correlated negatively against time than would be expected under their null hypotheses of ‘normal’ population fluctuations, with 67% of relationships being negative. However, they found no evidence that the *proportion* of populations decreasing changed over time – i.e. what one would expect if the proposed agents of decline were becoming more prevalent or intense. As the authors themselves admit, it is impossible to draw firm conclusions about the global status of amphibian populations due to variance in the size of data sets, their methodological origin, and the inter-specific variance in population dynamics which renders their null model far from perfect for all amphibian species. Houlahan *et al.* (2000) made by far the most exhaustive attempt to date in collating data from 936 populations of 157 species from 6 continents, for studies of between 2 and 31 years duration. Although their results identify marked temporal variation in the speed of the decline, and spatial variation as to its extent, a definite

negative relationship is clearly evident, adding perhaps the first real quantitative ‘weight’ to the declining amphibian phenomenon.

Aside from methodological problems, arising from sampling error, observer bias, and short time series (see below for further consideration), the detection of real population declines which are deserving of concern, from purely natural population fluctuations can pose a serious problem in monitoring programs. It is essential that we understand the natural levels of variability inherent in amphibian populations, so as not to invoke unnecessary conservation and management action – a result that could severely compromise support for conservation in other situations (Pechmann *et al.* 1991). There exist both temporal and spatial aspects of amphibian population dynamics that can serve to confound the attempts of many monitoring programs to elucidate real declines in number. Firstly, there is strong evidence of intraspecific density dependence in many amphibian populations (Berven 1990; Pechmann *et al.* 1991; Alford & Richards 1999; Meyer *et al.* 1998). Crucial life history factors that appear to be regulated by density dependence include larval survival, larval size and time to metamorphosis. Especially in a heterogeneous environment such as a forest, variance in such factors could produce seemingly chaotic fluctuations in population size (Turner 1962; Berven 1990; Pechmann *et al.* 1991). In the wood frog (*Rana sylvatica*) Berven (1990) recorded variation in R_0 (the net population replacement rate) between 0.009 – 7.49 over only 7 years, and as monitoring programs are rarely longer than this (Blaustein *et al.* 1994a; Alford & Richards 1999) it is easy to see how a short term population decline may be interpreted with unwarranted concern. Secondly, it is possible that at the level of the population, density dependent effects following fluctuations in resource levels may override the effect of any density *independent* environmental stress factors that may act to reduce juvenile or adult survival. However, as the judgement of ‘natural’ levels of stability in biological populations is exceedingly difficult to make (Connell & Sousa 1983), it is consequently difficult to identify the ecological significance of any such contribution to mortality or reduction in reproductive success to overall population dynamics, even though they may be non-trivial. Aside from density dependence, a second important consideration of the temporal dynamics of amphibians is in the fact that fluctuations in breeding aggregations may be much greater than fluctuations in total population size, due to intra-population variance in breeding behaviour (Pechmann *et al.* 1991). This point is of particular relevance, as due to severe logistical constraints most censuses of amphibians and especially frogs and toads (Amphibia: Anura), are conducted on aggregations at breeding sites (Alford & Richards 1999; see below).

Aside from temporal considerations one must also take into account the spatial aspects of amphibian population dynamics in making any conclusions about population stability or integrity. It is becoming increasingly recognised that many amphibian populations consist to a large extent of a metapopulation (see Hanski & Gilpin 1991) structure, where regional processes affecting extinction and colonisation of habitat patches, play a dominant role in determining local species assemblage composition and population size (Hecnar & M'Closkey 1996a; Alford & Richards 1999; Marsh & Trenham 2000). It is important to recognise that from the perspective of a monitoring program effective habitat 'patches' which are subject to such regional influences can represent the breeding sites or transects under human surveillance, and with respect to the actual amphibian population are often not ecologically distinct. The role of regional processes on the persistence of local populations means that local extinction can occur due to purely stochastic factors that are unrelated to the local environmental (abiotic or biotic) quality (Sjogren 1991). Amphibians are predisposed to local stochastic extinctions due to the susceptibility of a peak-breeding attempt to climatic conditions (i.e. droughts or floods), and their relatively short life spans (Marsh & Trenham 2000). However, the essential point is that although devastating reductions in population size may be observed at a particular monitoring site, at the regional spatial scale the species may be perfectly healthy, adding doubt to the extrapolation of many population censuses to conclusions about the viability of an entire species. In order to confidently assess the stability of an amphibian population, and attribute a reason to any observed decline, it is important that such spatial factors are considered (see below).

Candidates for amphibian decline

a) Habitat modification

The destruction or modification of ecological systems is widely held as the primary cause for the observed loss of much of the earth's biological diversity, and the loss of amphibian species and reductions in their population size bear no exception (Alford & Richards 1999). In an area directly under human influence, habitat modification can usually be isolated as the cause of an observed population decline, although the actual mechanism is highly variable and can often be obscure. Short of complete human development, more common modifications include; (1) forest management operations resulting in a change of microclimate, soil moisture and habitat complexity, (2) land drainage for reservoirs and other developments, resulting in a removal of breeding sites and

fragmentation of populations, and (3) the alteration of the biotic environment, through the introduction of exotic predators and pathogens (see below). More obscure and perhaps counter-intuitive examples exist, such as in the case of the natterjack toad (*Bufo calamita*) in Britain, where the *removal* of management (grazing) on shrub heathland led to the encroachment of tall vegetation, thus allowing the entrance of the more successful competitor *Bufo bufo* – the common toad (Beebee 1977). Such examples serve to emphasise the fragility of many ecological systems to what we may perceive to be minimal human intervention. However, habitat destruction and modification although of prime concern, are usually easily to isolate, and therefore if possible, to rectify. It is the proposal that amphibian declines in largely pristine areas of the world are the result of more esoteric and perhaps nebulous reasons that is cause for exceptional concern.

b) Ultraviolet radiation

Depletion of the stratospheric ozone layer and the observed resultant increases in ultraviolet B (UV-B) radiation at the earth's surface (Kerr & McElroy 1993), has prompted interest as to the possible relationship between the influence of UV-B on amphibian survival and population declines. A number of experimental manipulations of enhanced UV-B have implicated its potential contribution to amphibian declines through evidence of; decreased hatching success (Blaustein *et al.* 1994c; Ovaska *et al.* 1997; Anazalone *et al.* 1998), enhanced embryonic mortality (Anazalone *et al.* 1998), decreased larval survival (Ovaska *et al.* 1997), and negative effects on embryo and larval development (Crump *et al.* 1999). However, all of these studies report significant variation between species as to both the level and type (i.e. embryo, larvae etc) of susceptibility. Some resolution of this discrepancy has been proposed through inter-specific variation in the levels of the DNA repair enzyme, photolyase (Blaustein *et al.* 1994c; Blaustein *et al.* 1996). Indeed a correlation can be made between a number of species whose populations are showing a decline in number (e.g. *Bufo boreas* and *Rana cascade*) and which also show significantly low levels of photolyase activity. This can be compared against species such as *Hyla regilla* which has characteristically high levels of the enzyme and exhibits relative stability in number (Blaustein *et al.* 1994c). However, this relationship is clearly not of global relevance as the Red-legged frog *Rana aurora*, has a relatively high level of photolyase but yet has suffered severe depletions in number (Blaustein & Wake 1990; Blaustein *et al.* 1996). A further quite equivocal result is seen in the declining Australian species, *Litoria aurea*, which although has a lower photolyase activity than is two sympatric non-declining species, *L. dentata*, and *L. peroni*, shows no significant difference against them with respect to hatching success under enhanced UV-B exposure

(van der Mortel *et al.* 1998) – thus pointing to the importance of other, independent agents of decline.

A number of other factors serve to shed doubt on the responsibility of UV-B in global declines. Most of the field experimental studies cited above have been conducted in shallow, clear high altitude ponds, largely in high latitude locations such as North America and south-eastern Australia. UV-B radiation is largely absorbed in the first few centimetres of the water column (Nagle & Hofer 1997), and the depth of penetration is negatively correlated against the dissolved organic carbon content (Crump *et al.* 1999) – factors which suggest that UV-B radiation is unlikely to be a problem in bottom laying species, or in forest (and especially tropical) species. A lack of evidence for significant increases in UV-B at tropical or sub-tropical latitudes since the mid-1970's (Madronich & Grujii 1993) further diminishes its likely role in the decline of tropical amphibian populations (e.g. Crump *et al.* 1992; Lips 1998).

Although some of the above evidence is convincing in showing an effect of high UV-B radiation on embryo mortality and larval survival, the ecological significance of such a phenomenon at the population level is far from clear, and equally difficult to assess (Alford & Richards 1999). For example there may be density dependent compensation effects, through the enhanced fitness of competing individuals that survive high levels of UV-B exposure. The potential indirect effects of enhanced UV-B on amphibian dynamics, such as changes in water chemistry and food supplies, are even less well known (Alford & Richards 1999). Finally it appears likely that unimodal experiments manipulating only levels of UV-B are inadequate, and that the crucial agent of decline could be in the synergy of UV-B with other key environmental stresses (see below).

c) Acidification and toxins

The existence of amphibian extinctions and population declines in what are otherwise seen to be some of the most pristine environments on Earth has prompted the putative role of atmospheric pollutants as agents of decline (Lips 1998). Such pollutants could originate from neighbouring and foreign agricultural depositions, as well as from factory emissions of industrialised nations, and are able to travel vast distances and persist for considerable periods of time. One of the most acknowledged remote impacts of human activity is increased acidity of rainfall, a phenomenon of great potential importance in light of the significance of the annual water regime to amphibians.

Increased acidity of ground and pond water is suspected to have both lethal and sub-lethal effects on amphibian populations through a number of factors; enhanced embryo and larval mortality, reduced egg and larval growth, reduced reproductive output, delayed hatching times, reduced adult body size, alterations in geographic distribution, and alterations in predator-prey ratios through indirect effects on plant growth and pH sensitive competitors and predators (Freda & Dunson 1986; Alford & Richards 1999). Some field and laboratory work has provided evidence for such detrimental effects, for example; reduced ion exchange and larval growth in *Rana sylvatica* (Freda & Dunson 1986), and a significant reduction in range size of *Bufo calamita* following long term acidification of many British ponds (Beebee *et al.* 1990). Some evidence also exists for the potential role of another major pollutant, pesticides, in stimulating amphibian declines, with significant effects being observed on crucial population regulatory processes such as juvenile recruitment under enhanced pesticide levels (Bridges & Semlitsch 2000). The marked interspecific variation of amphibians in their susceptibility to pesticides alongside geographic variation in their deposition is highlighted as a potential explanation for the heterogeneous nature of observed declines at both taxonomic and geographic scales (Bridges & Semlitsch 2000).

Although it is clear from the above examples that an increase in environmental acidity or other pollutants can have a negative effect on some amphibian populations, the actual physiological mechanisms remain unclear (e.g Carey *et al.* 1999). Furthermore, and perhaps most crucially, it is once again not evident what the overall consequences of such environmental changes at the population level would be, and there is very little data implicating contaminants on the recent catastrophic population declines (Alford & Richards 1999). However, as in the case for enhanced UV-B levels, it is possible that the critical role of environmental contamination in population declines comes from its *interaction* with other causative agents (see below).

d) Predation

Biotic interactions amongst and between biological species can play a critical role in determining their relative local abundance, distribution and population dynamics (Ricklefs & Schuler 1993; Huston 1994). Although perhaps more appropriately considered as human induced habitat modification, the introduction of exotic predators to amphibian environments has been implicated as the factor responsible for many declines, including the collapse of whole communities (Fellers & Drost 1993; Fisher & Shaffer 1996; Hecnar & M'Closkey 1996b). Aside from such co-incidental

evidence, experimental manipulations of predator and amphibian distributions provide firm support to their devastating effect on amphibian populations. Two good examples are the significant reduction in survival of the endangered Red-legged frog (*Rana aurora*) in California, following the introduction of the two larval predators - Mosquitofish (*Gambusia affinis*), and Bullfrogs (*Rana catesbeiana*) (Lawler *et al.* 1999), and secondly, a severe impact of both Mosquitofish, and a crayfish (*Procambarus clarki*) on the eggs and larvae of the Californian newt, *Taricha torosa* (Gamradt & Kats 1996). Although the introduction of exotic predators such as the above is considered to be a prime cause of decline across North America (Fisher & Shaffer 1996), their role is usually easily identified, and as such seems unlikely to be a global factor, especially in largely pristine tropical areas.

e) Disease

The remote nature of many amphibian population declines, in addition to the frequently observed larval and adult growth abnormalities has led to the perhaps unsurprising widespread suggestion as to the role of disease – either following exotic introduction or an increased virulence / compromised immunity. In particular the wave-like nature across species ranges of many declines, as observed in both the Atlantic forest of Brazil (Heyer *et al.* 1988), the Eastern montane forests of Australia (Laurance *et al.* 1996), and the forests of Panama and Costa Rica (Lips 1998, 1999), has prompted the role of a biotically induced agent of decline – i.e. disease. Perhaps the most confident proposition as to the culpability of disease in precipitating the collapse of an entire amphibian community is in Australia, where 14 endemic species have decreased by more than 90% in the last 15 years (Laurance *et al.* 1996). The authors note the extreme virulence of the disease as being evidence of its potential exotic nature, and report histological changes in infected tissue of diseased individuals as being consistent with viral infection. Lips (1998, 1999) identified a fungal infection found on dead individuals as being the most likely cause of population decline in the forests of Panama, between 1993 and 1997. Furthermore she notes that the similarity in timing of declines, regional climatic factors, frog phylogenies, and clinical symptoms, as being suggestive of the same causal factor being responsible for catastrophic amphibian declines noted in nearby Costa Rica (Pounds & Crump 1994; Lips 1998). Support for this theory comes from Berger *et al.* (1998) who identified the same chytridomycete (Chytridiomycota: Chytridiales) fungus on dead anurans from forests of both Central America, and also of Queensland, Australia – adding some further strength to the argument of Laurance *et al.* (1996) although the disease origin differs. The identified fungus is known to be globally widespread, and the relatively sudden observation of catastrophic declines in

such disparate areas of the world is suggestive of a recent increase in virulence, or decrease in amphibian immunity, perhaps due to an interaction with a changing global climate (see below). Further convincing evidence as to the role of disease in population declines comes from the Pacific north-west of America, where a different species of fungus, *Saprolegina ferax* which is a world-wide fish pathogen, has been implicated as responsible for declines in *Bufo boreas*, through increased egg mortality (Blaustein *et al.* 1994b; Kiesecker & Blaustein 1997).

There is clearly enough convincing evidence to support the two facts that disease agents can be highly detrimental to amphibian fitness and survival, and that furthermore, evidence of them can be found in many areas where catastrophic declines have occurred. However, as for most if not all agents of decline, it is very difficult to attribute what contribution they make to the overall population dynamics of declining amphibians. Strong circumstantial evidence exists as to the role of disease in mass declines such as that observed in Australia (Laurance *et al.* 1996). However, when strong experimental proof is difficult to obtain, it is easy to argue for competing hypotheses which may well produce equally parsimonious statistical comparisons of a potential agent of decline against the spatial distribution of amphibian population declines (Alford & Richards 1997; Hero & Gillespie 1997). Despite this ubiquitous presence of a large range of competing hypotheses to explain any one population decline, it is crucial to the progress of science that plausible hypotheses are voiced, if only for their heuristic value in targeting future research and formulating further, refined hypotheses (Laurance *et al.* 1997). As noted below, in the case of disease it is even more likely than in other agents of decline, that interactions of disease vectors with other environmental factors plays a crucial role in determining their impact on amphibian populations.

f) Climate and weather

As discussed above amphibians are particularly sensitive to their external environment, both due to their biphasic lifestyle in existing as both aquatic larvae and terrestrial adults, and due to their highly permeable skins. Perhaps the most important component of the abiotic environment to both amphibian fitness and population dynamics is the maintenance of a stable and predictable water-temperature regime (Pounds & Crump 1994; Lips 1998). Many amphibians are subject to both water and temperature sensitive physiological limitations on locomotive and reproductive activities. As a consequence of this the balancing of evaporative water loss against direct absorption through the skin is critical functional attribute, as has been observed in the marine toad *Bufo marinus* (Pounds

& Crump 1994). Aside from detrimental effects of disrupting this balance (i.e. through desiccation), at the individual level, the water regime in particular can play a vital role in many other aspects of amphibian ecology, including; (1) determination of phenological patterns of reproductive activity (Wells 1977; Aichinger 1987; Gascon 1991), (2) determination of the spatial distribution of community assemblages (Ingler & Voris 1993), and (3) in the provision of suitable breeding sites and conditions (e.g. Pyburn 1970).

The suspected role of alterations in the annual water regime of amphibians in global population declines, follows increasing recognition of gradual changes in the global climate due to human activities. There has been a discernible human influence on world temperatures during the last century, with average temperatures projected to increase by between 1 and 3.5°C by 2100, with considerably greater regional variation (IPCC 1995). One consequence of this that is relevant here is a projected increase in activity of the tropical hydrological cycle, with the prediction of erratic and frequently severe weather patterns (IPCC 1995; Graham 1995). The effect of climatic change on ecological systems has been observed at all levels, from population and life history alterations, to shifts in geographic range, and subsequent changes in community composition resulting in disruption of ecosystem structure and function (Hughes 2000; McCarty 2001). It is therefore perhaps unsurprising that many changes in the population dynamics of amphibians, organisms which are so closely coupled with their environment, have been attributed to changing climatic and weather patterns.

A number of notable reports documenting multiple amphibian declines have implicated the potential role of synchronously observed climatic extremes, and in particular, periods of reduced or abnormally distributed rainfall (Heyer *et al.* 1988; Crump *et al.* 1992). Owing to the sensitive response of amphibian breeding cycles it is easily conceivable that a simple shift in the commencement of the wet season in seasonal environments could either trigger premature spawning and subsequent desiccation of eggs, or if early rains are abnormally intense, the flooding of breeding ponds, and an equally disastrous loss of an entire breeding attempt (Wells 1977; Crump *et al.* 1992). Pounds & Crump (1994) executed a more detailed analysis of the infamous declines in number of Golden toad and Harlequin frog populations in the Monteverde cloud forests of Costa Rica, and concluded that coincidentally low periods of rainfall during phases of population decline were at least in part responsible. It was clear that depletions in number of the Harlequin frog populations

(for which demographic data was available) matched climatic records of reduced rainfall during both the 1982-1983 and 1986-1987 El Niño induced drought periods. The potential role of long-term warming and increased intensity of precipitation patterns, when coupled with intense warm periods of El Niño/Southern Oscillation cycles, has been noted to be of severe consequence for many biological communities (McCarty 2001), and in light of the above, particularly so for amphibians (Pounds 2001). With particular reference to the example of Crump *et al.* (1992) and our own study, it has been recently calculated that the effect of El Niño events in Central America is expected to be through severe drought periods rather than increased rainfall (Holmgren *et al.* 2001). Although the juxtaposition of the timing and extent of population declines in Harlequin frogs with the timing and intensity of periods of drought suggests that they are causally linked, it is much more difficult to identify either the environmental variable that is of crucial ecological significance, and further the exact mechanism by which that change acts to reduce amphibian populations. Pounds *et al.* (1999) in a further analysis of the situation in the Monteverde cloud forests, isolate a perhaps rather unintuitive climatic variable as being closely correlated with not only amphibian declines but also with demographic changes in many other taxa, including birds and reptiles. The climatic variable is that of *dry season mist frequency*, which suggests that the important water-related *mechanism* affecting amphibian populations is likely to be an increase in desiccating conditions affecting egg hatching in non-aquatic species, alongside individual survival, rather than changes in reproductive phenology and breeding behaviour. Human induced climate change can be implicated here, as dry season mist frequency is negatively correlated with sea surface temperatures of the equatorial Pacific, which have increased dramatically since the mid-1970's (Still *et al.* 1999). Such examples highlight the importance of studying the environment of a species under threat so as to identify the ecologically important variables, and allow an assessment of future population stability through the parameterisation of predictive ecological models – both verbal and mathematical (McCarty 2001).

Aside from the above, a number of other mechanisms have been suggested to explain the potential role of climatic change in precipitating amphibian population declines. A shift in rainfall patterns could result in a change in availability of breeding sites, a reduction in which could increase levels of competition and predation, and even vulnerability to disease, resulting in a reduced overall reproductive output for that year (Donnelly & Crump 1998). An increased frequency of drought periods, coupled with increased temperatures, have also been identified as having potentially severe effects on leaf litter species which don't congregate to breed, through alteration of their arthropod

prey base and an increase soil desiccation (Donnelly & Crump 1998). Finally, there is evidence of changes in spring spawning times of amphibian species in England, showing that amphibian reproductive cycles are highly sensitive to climate warming, with possible long-term consequences for population dynamics through alterations of biotic interactions (Beebee 1995). However, as with all the potential agents of amphibian decline listed above, changes in climatic patterns can not always be found to explain observed declines (e.g. Laurance 1996). Furthermore, due to the close coupling of amphibian population dynamics to their ecological environments, it is likely that any climatic change would effect amphibians through interactions with other biotic and abiotic factors, to which both the external climate and amphibians themselves are closely linked.

g) Interaction effects amongst environmental factors

Frequently the separation of the almost myriad of current hypotheses for amphibian declines in any one situation can be almost impossible, although some recent advances have been made using GIS technology to compare spatial patterns of decline with spatial patterns of potentially causal agents (Davidson *et al.* 2001). However, as noted above most of the studies to date that have considered a single causal mechanism behind amphibian declines have invoked a critical interaction between multiple factors (Alford & Richards 1999). Such acceptance means that despite the urgency of explaining observed declines, it is important to realise that interacting suites of environmental change could produce complex effects that are difficult or even inappropriate to isolate (Adams 1999).

A number of recent experimental and observational studies offer support to the importance of interaction and synergistic effects between different hypothetical agents of decline. Increased UV-B exposure has been shown to increase the susceptibility of some amphibian species to disease (Kiesecker & Blaustein 1995; Kiesecker & Blaustein 1997). Furthermore an increase in UV-B can act synergistically with reduced pH levels to reduce embryo survival, when each factor alone is shown to have no significant effect (Long *et al.* 1995). Normally harmless diseases may increase their effective virulence under increased environmental pollution by contaminants such as pesticides (Bridges & Semlitsch 2000), and even different diseases themselves can be seen to act in concert in order to produce a detrimental effect (Cunningham *et al.* 1996). Although an established (native) pathogen itself may be insufficient to significantly alter the dynamics of amphibian populations, a differential effect amongst competitors can produce strong changes in the strength and direction of

biotic interactions, thus altering an original hierarchy of competitive ability, and therefore the relative abundance of each species (Kiesecker & Blaustein 1999). Although the exact mechanisms are not well understood (see above), it is likely that global climate change can interact importantly with virtually all local factors with respect to their effect on amphibian populations (Pounds 2001). For example an increase in drought events and the subsequent loss of many ponds and breeding sites, could greatly exacerbate the effects of local predators (Drost & Fellers 1996). Also an increase in temperature can increase the volatility of potentially harmful chemical deposits, the aerial concentration of which may then be increased due to a reduced frequency of rainfall events (Pounds & Crump 1994). Due to the sensitivity of many ecological systems to climatic change (McCarty 2001), it is likely that alterations of key environmental variables such as rainfall patterns and temperature, have the effect of reducing or even removing an important constraint on the *potential* of many agents of decline, both with respect to their geographic distribution but also in their physiological or biotic effect (e.g. UV-B, pH, disease) (Pounds 2001). Just how complex an effect such changes in climatic parameters can precipitate has been illustrated in a very recent study by Kiesecker *et al.* (2001). Their findings illustrate that climatic induced reductions in water depth at amphibian oviposition sites have caused a high level of mortality in embryos, by increasing their exposure to UV-B radiation, and consequently their vulnerability to infection by disease. The implication of this is that elevated sea surface temperatures in the tropical Pacific, which drive large scale climatic patterns, could be the precursor for many pathogen-mediated amphibian declines world-wide (Kiesecker *et al.* 2001).

It should be clear from the above discussion that observed amphibian population declines seem unlikely to be the result of a small number of independent global agents, but rather the complex interaction of local effects in the context of varying regional influences and global climatic change. In order to study the existence of such effects in natural populations, and thus elucidate the relative stability and integrity of such populations, well-planned programs of observation and experimentation are needed (Alford & Richards 1999). Furthermore, in light of the importance of both abiotic but also biotic interactions, it is important to gain an understanding of the interactions of the populations under study with both other species (amphibians and other potential competitors and predators), and their physical environment. Finally in order to identify the existence of a real population decline with confidence, development of specific 'null' hypotheses or models is needed to describe how amphibian populations behave in the absence of external pressures.

Monitoring of amphibian populations: points to note

In studying the proposed phenomenon of global declining amphibian populations, there are perhaps three main questions in which uncertainty remains; (1) How to determine real declines from natural population fluctuations?, (2) Whether human induced agents can be isolated as the potential cause of the decline?, and (3) Whether global agents are responsible for the majority of observed declines?. In light a growing recognition of the important implications of the mounting extinction crisis (see above), we cannot afford to be either complacent or conservative in our approach towards answering such central questions. In view of this there is a desperate need for comprehensive monitoring studies on amphibian populations world-wide (Blaustein *et al.* 1994a; Wake 1998). As can be seen from recent compilations of studies to date by Alford & Richards (1999) and Houlihan *et al.* (2000), they exhibit a notable disparity with respect to length, scope, and detail. In order to draw firm conclusions at both the local and global level, it is imperative that future studies build upon previous work, and where possible incorporate recent advances in our understanding of amphibian species and their population dynamics. It is therefore instructive here to draw attention to a number of considerations additional to those already noted above.

The natural variability and complexity that is inherent in both temporal and spatial amphibian population dynamics has already been highlighted above. It is crucial to recognise that such factors introduce serious practical considerations and caveats in the construction, execution, and analysis of amphibian monitoring programs. A direct consequence of such natural levels of variability is that the failure to find a significant decline in number of a particular population may frequently not be due to a lack of real decline, but rather to a lack of statistical power (Reed & Blaustein 1995; Hayes & Steidl 1997; Alford & Richards 1999). The statistical power of a test for a population decline can be defined as the probability of rejecting the null hypotheses of no decline given that the null hypothesis is false and the alternative hypothesis of a declining population is true. Calculation of power requires knowledge of a number of factors, namely the sample size, the desired alpha level for avoiding Type I errors, the natural variance in sample size, and the effect size (Peterman 1990). The value of conducting a prospective power analysis (Hayes & Steidl 1997) is severely limited by the high level of uncertainty inherent in the last two factors; (1) the natural variability in amphibian populations – in particular in the context of the specific monitoring approach being used, and (2) the level of population decline (effect) which bears ecological significance for the future stability of an

amphibian population. We would venture that in light of the serious logistical and financial limitations imposed on many, if not most amphibian monitoring projects, the ‘guesstimating’ of such variables is a dangerous game as it may render void many otherwise valuable projects which are lacking in statistical rigour (and crucially lacking in ability to expand the project’s sample size to achieve a satisfactory level of power). Except in situations where the species under surveillance is well studied, it may be of greater *ecological* significance to take a comprehensive approach to monitoring which incorporates a number of key ecological, as well as methodological considerations. This will hopefully achieve an increased understanding of the environmental requirements and population dynamics of the specific focal species, and afford greater confidence in any data interpretation. That is not to nullify the clear value of prospective power analysis, rather to opine that there is a great deal of merit in carefully considered monitoring projects which do not yet hold the minimum level of information needed to make such a preliminary analysis worthwhile. Identified below are some of the considerations deemed central to amphibian population monitoring.

For reasons emphasised earlier the two main problems facing monitoring projects are the logistical constraints on their temporal and spatial focus. Clearly in order to elucidate real declines from stochastic fluctuations, a long time series is highly favourable, although as seen from recent literature reviews few studies are longer than 5 years, and even less are more than 10 (Alford & Richards 1999; Houlahan *et al.* 2000). Secondly, in light of the metapopulation structure and the critical role of processes such as emigration and colonisation in amphibian populations, a regional monitoring perspective is important in order to distinguish overall regional declines from local (and essentially stochastic) extinctions (Marsh & Trenham 2000). For most amphibians this requires an appreciation as to the importance of the spatial arrangement, and degree of isolation, between different breeding sites. It is appropriate to note here that according to a recent review of techniques used to quantify amphibian populations, most attempts focus on direct or indirect (e.g. vocal calls, egg masses) counts at breeding sites (Alford & Richards 1999)– utilising the fact that most species congregate *en masse* to breed (Beebee 1996). It thought that the population dynamics of a species are determined primarily by recruitment processes occurring at breeding ponds, and that such a focus can accurately determine the cause of any local or regional decline (Marsh & Trenham 2000). However, such an exclusive focus carries a number of caveats in data interpretation; (1) Variation in population size at breeding ponds can as well be due to variation in breeding behaviour as to actual variation in population number (Pechmann *et al.* 1991), (2) It is often impossible to clearly distinguish variation

in *population* size from simply variation in the size of breeding aggregations – ie the degree of ‘openness’ of the population (McArdle & Gaston 1993). Both such measures represent useful information but it is important to note that they are not synonymous. (3) In terms of adult survival and distribution an exclusive focus on breeding sites ignores the potential importance of the intervening terrestrial habitat which may be of ecological significance (Marsh & Trenham 2000). A final note with respect to natural variability in amphibian populations is interspecific or taxonomic variance. As emphasised earlier different species exhibit different levels of susceptibility to different agents of decline. Accordingly any attempt to assess the stability or vulnerability of an amphibian fauna at any one site should consider not only the breadth of species present, but also a number of different populations of each. With relevance to all levels of variability that can serve to confound attempts to identify declining populations, a high number of intra-annual repeat visits to each monitoring site (especially during the peak breeding season) can add important, if not essential strength to the results Alford & Richards 1999).

Alongside data on the population dynamics of the focal species, it is important to gain an appreciation of the differential importance of key ecological variables in both the biotic and abiotic environment (e.g. climate, water quality, floral composition, and predator abundance). Such a multidimensional approach to monitoring helps to identify any potential agents of decline, but also to help predict any secondary effects or feedbacks following a potential change in the structure of the amphibian community. This information, when integrated into demographic data of the amphibian populations can be invaluable in building a null model to predict the range and patterns of population behaviour in the absence of external pressures or agents of decline (Alford & Richards 1999). Such null models can be used to reduce the subjectivity and ambiguity that often surrounds the evidence for a population decline (Pounds *et al.* 1997).

Chapter 2: The role of Project Anuran

Although the declining amphibian phenomenon is virtually undisputed, there remains a critical demand for quantitative work to assess the geographic and taxonomic variation in both the extent and nature of population declines. Through the intensive monitoring of an entire anuran (Amphibia: Anura) fauna at the tropical site of Las Cuevas, Belize, Project Anuran aims to respond to this demand by providing information on the population dynamics, reproductive behaviour, and environmental requirements of all local species throughout each wet season. Our study serves to complement existing work by concentrating on both an area and species assemblage that remain largely unstudied.

Due to the spatial distribution of amphibian biologists much of the work on declining populations to date has been in North America, Europe and Australia (Houlahan *et al.* 2000). A consequence of this is that there is a desperate need for more studies from other areas of the world, and in particular from the highly diverse regions of the tropics (Wake 1991; Pearman *et al.* 1995; Wake 1998; Houlahan *et al.* 2000). In light of the concern surrounding amphibian declines in regions thought to be pristine from human influence (e.g. Crump *et al.* 1992), it is appropriate to consider the potential role of global factors in some of the most pristine environments remaining on Earth – those of tropical forests (Groombridge & Jenkins 2000). In the context of our work, the forests of the neotropics harbour a great diversity of amphibians (Lee 1996), and although a number of studies have been conducted at high altitude locations (e.g. Guyer 1990; Crump *et al.* 1992; Lips 1998), very little has been done in lowland regions (Wake 1998). Belize contains some of the most extensive and valuable stretches of forest in Central America (Furley 1998), retaining some 75% of its natural vegetation (Harcourt 1994), and as such providing a haven for much of the wildlife that has vanished from other neighbouring countries (Romney *et al.* 1959; Hartshorn *et al.* 1984). However, the ecology of many amphibian species in Belize remains largely unknown (P.J. Stafford and J.R. Meyer pers. comm.), a statement that is strengthened by the fact that 5 out of the total 33 species of anurans in Belize were discovered between 1990-1995 (Meyer & Foster 1996). Although no species in Belize are listed as vulnerable or endangered by the IUCN, this is no justification for an absence of monitoring programs. It is of unarguable importance that the study of a potentially global phenomenon is not restricted to areas where its symptoms are evident (e.g. Monteverde in Costa Rica). Furthermore, if global climate change is indeed a central factor behind amphibian declines, it

is perhaps *more* important to consider those species that have so far shown no response to changes in temperature and rainfall – perhaps giving different and more ominous implications for their future conservation (McCarty 2001).

The DAPTF are presently co-ordinating a monitoring program entitled the Maya Forest Anuran Monitoring Project (MAYAMON), as part of a large, internationally funded biological monitoring project of the entire Selva Maya region (Carr & de Stoll 1999). The information collected by Project Anuran is fed into a regional picture collated by MAYAMON using data from studies throughout Belize, the southern states of Mexico, and the Péten region of Guatemala. Our study site of Las Cuevas is able to provide a good comparison against many more disturbed areas in other parts of the region. However, we feel that perhaps our most significant contribution to an increased understanding of the declining amphibian phenomenon, is due to the fact that undergraduate projects such as ours are able to offer a considerable amount of time, personnel, and resources to allow for an effective comprehensive monitoring program – a achievement that is beyond the reach of many professional ecologists for very practical reasons of time and logistics. Although ideally monitoring projects need to cover at least a few adult generations, both funding constraints and the urgency of the situation usually preclude this approach. It is therefore optimal to have a program which focuses on a whole community of amphibian species, over a number of breeding sites, and incorporates consideration of detailed abiotic and biotic environmental variables on a frequent basis.

Aims and Objectives

Research Aim

“To contribute to the understanding of the ecology and conservation of amphibian populations via an intensive monitoring program of the anuran (Amphibia: Anura) fauna at the neo-tropical site of Las Cuevas, Belize (N16°44' W88°59').”

Research Objectives

1. To monitor changes in assemblage composition and relative abundance of vocalising anurans throughout the entire night and the duration of the wet season, across eight breeding sites in the vicinity of Las Cuevas
2. Further to Objective 1, to monitor differences in the abiotic (including climate variables, and water quality) and biotic (floristic composition, predator abundance) environments between breeding sites, and across time.
3. Using a number of complementary methods, to monitor the diversity, relative abundance, and habitat associations of leaf litter species, mainly of the family Leptodactylidae. Further, to comment on the relative effectiveness of standard methods used to assess this highly cryptic group.

Further Aim

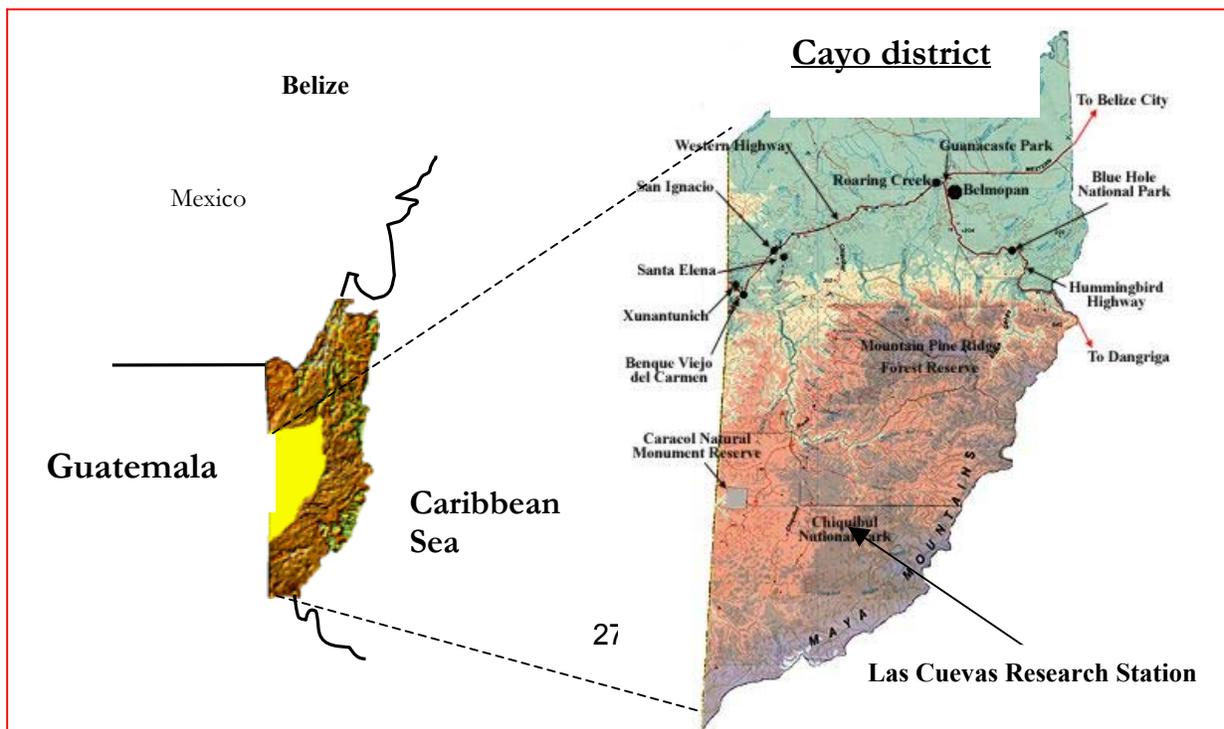
“To continue efforts to establish firm links with a collaborative student group from the Belize, with an aim to consolidating closer ties between the student community from both countries who are concerned about ecology and conservation management in Belize.”

Chapter 4: Methodology and approach

Site description

Our work was conducted in the vicinity of Las Cuevas Research Station (N16°44' W88°59') which represents a joint venture between the Natural History Museum (London) and the Forestry Department of Belize. The research station is situated in the Chiquibul Forest Reserve, lying within the much larger protected area of the Chiquibul National Park and the Maya Mountains— see Map 4.1. It stands at roughly 500 m a.s.l with an annual rainfall between 1500 and 2000 mm, with vegetation consisting mostly of lowland subtropical moist forest (Hartshorn *et al.* 1984). Due to its largely pristine nature, and high level of biodiversity, the Chiquibul forest represents one of the most ecologically important forests in Belize (Bird 1998). With respect to the anuran fauna, the Maya Mountains is one of the most diverse regions of Belize (Miller & Miller 1995), containing 5 species that are found nowhere else in the country (Lee 1996; Meyer *et al.* 1999). Since the collapse of the Mayan civilisation around AD 900 there have been no permanent inhabitants of the region around Las Cuevas. However, the area has received a number of disturbances, both natural and human. Selective logging of mahogany (*Swietenia macrophylla*) and cedar (*Cedrela odorata*) occurred between 1936-46 and again in the late 1980's. The forest has been used by local people as a source of chicle (the latex of the sapodilla tree) and bayleaf palm thatch. Hurricanes have caused widespread destruction in the area over its recent history – namely in 1942 and 1961 – and large forest fires are not an uncommon occurrence

Map 4.1 : The location of Las Cuevas Research Station



The methodologies used in the project fall under two sections; those pertaining to the monitoring of vocalising species, and those pertaining to monitoring of non-vocalising species.

Weather

Daily recordings at 0900 hours were made of rainfall (mm) and maximum/minimum temperature for the previous 24 hours. These were made using a standard rain gauge and thermometer at the Las Cuevas weather station. Further measurements were taken of the duration of each rainfall event to allow a measure of rainfall intensity to be calculated to compliment the basic measure of volume.

Field study 1: Vocalising species

Most anurans species, especially in the tropics congregate *en masse* around breeding sites to mate (Duellman & Trueb 1994; Beebee 1996). It is therefore unsurprising that the majority of studies attempting to quantify amphibian populations are conducted at breeding sites (Alford & Richards 1999). Although a number of methods have been attempted, including mark-recapture, direct counts, and indirect counts of egg masses, the arboreal nature of many of the species along with their small size, and nocturnal habit, means that monitoring group vocalisation is frequently the most effective technique (Alford & Richards 1999). We chose eight breeding sites, representative of a number of different microhabitats of the forest around Las Cuevas. The main habitat features which distinguish the ponds, are the degree of canopy cover, density of understory vegetation, and distance to a clearing. Pond site selection was made following advice from local guides, and night walks around the area. The position of these sites is shown on Map 1 of the Appendix. Each pond was surveyed at least three times at roughly even intervals throughout the study period of 6th July to the 3rd September 2000. Each survey ran from 1900 hours to at least 0200 hours, with a number of ponds being surveyed until 0500 depending on the extent of frog activity. Measurements taken at the start of each survey night included; depth of pond (deepest point), pH sample, and a summary weather report. Further environmental measurements were taken hourly from 1900, including; air

temperature, water temperature, relative humidity (using a whirling psychrometer), and volume and duration of rainfall that fell during the previous hour. These environmental measurements follow standard recommendations for monitoring amphibian species (Heyer *et al.* 1994), the MAYAMON protocol (Meyer 1999b), and a number of recent monitoring projects analogous to ours (e.g. Guyer 1990; Gascon 1991). Alongside the environmental measurements hourly recordings were made of the diversity, relative abundance, and calling activity of all frog species present. Measures of abundance followed the MAYAMON protocol (Meyer 1999b), the collaborative organisation to whom our results feed directly. This method uses vocalisation categories to assess the abundance of each species during the first fifteen minutes of each hour:

- **1 = 1-5 individuals**
- **2 = 6-20 individuals**
- **3 = 21-50 individuals**
- **4 = >50 individuals**

It is important to note here that although these categories are quite broad, they allow for a rough but *accurate* and *repeatable* measure of the number of frogs present of each species. It is important to not sacrifice accuracy here for numerical precision – i.e. we follow the motto that it is far better to be roughly accurate than incorrectly precise, especially when it comes to data analysis and interpretation. Measurements of the vocalisation activity of each species were recorded to allow an assessment of temporal dynamics of reproductive activity over and above simply species presence and absence. This was done using a measure (analogous to the above) of calling intensity - measuring the frequency of calls of an average individual of each species, for the first fifteen minutes of every hour. One call was taken as each noticeably distinct vocalisation per individual, a definition which serves well for the majority of species, with some notable exceptions (see below)

- **A = 1 or < 1 calls per 15 minutes**
- **B = 2-14 calls per 15 minutes**
- **C = 5-10 calls per 5 minutes**
- **D = 2-5 calls per minute**
- **E = 6-10 calls per minute**

- **F = 11-20 calls per minute**
- **G = 21-40 calls per minute**
- **H = >40 calls per minute**

Values observed for the entire night were; maximum and minimum temperature, volume of rainfall and duration and number of rainfall events. An example survey sheet for a typical vocalisation survey is given in the Appendix. For each pond an assessment of the floral diversity was recorded. This was done by mapping the area surrounding the pond and noting all tree species with a DBH > 10cm within 10m of the pond edge. Floral mapping of this nature allows an insight into the potential contribution that the local plant species composition has towards structuring the amphibian species composition present.

Identification of vocalisations in this study followed reference to a tape produced by Jack Meyer and Julian Lee. Our own recordings were made using a Sony minidisc and Sony microphone, the compilation of which will be used for future field phases of Project Anuran.

In addition to the standardised survey protocol outlined above all anecdotal recordings of these species were noted, separately, detailing the place of observation, species type and number, weather conditions, and any relevant natural history notes.

Field Study 2: Non-vocalising species

The study of leaf litter frogs of the neotropical family Leptodactylidae (which includes the world's largest vertebrate genus, *Eleutherodactylus*) has proved to be of considerable difficulty to researchers owing to the highly cryptic nature and nocturnal habit of many of the species (see Pearman *et al.* 1995). Our methods of intensively searching forest plots follows the standardised protocol outlined by Heyer *et al.* (1994). The majority of effort in assessing this species centred on searching 51 plots of 8 m x 8 m. To position these plots, the existing paths of the area were utilised to provide an access framework. Every 400m along the path a plot was placed, and a random selection procedure was used to determine the direction away from the path (left or right) and the deviation into the forest (max. 50m). This allowed sampling of the leaf litter amphibians from an area 100m wide by approximately 15km long. Appendix Map 1 illustrates the position of each plot. Eight plots along

the Monkey Tail branch of the Raspaculo River and ten plots in the vicinity of the Rio Frio River were also searched but are not shown on Appendix Map 1. Plot searching was conducted on average every second evening between 1800 hours and midnight, employing four people to systematically search the whole area, working into the centre in a concentric pattern, turning over all leaf debris, logs and loose rocks. Alongside the date and duration of the search a number of environmental variables were recorded at each plot site. Justification for these variables follows standard recommendations for monitoring amphibian species (Heyer *et al.* 1994), the MAYAMON protocol (Meyer 1999b), a number of recent monitoring projects analogous to ours (e.g. Guyer 1990; Gascon 1991), and anecdotal observations of our own following observation of leaf litter frogs under particular habitat conditions. The variables are:

- Species present, their abundance, an estimate of snout vent length (SVL) and example photographs
- Summary weather report; including cloud cover and time since last rainfall
- Phase of the moon
- Air temperature
- Relative humidity (using a whirling psychrometer)
- Leaf litter depth and % ground cover
- % canopy vegetation cover
- vegetation type (% contribution of herbs, shrubs/small trees and mature trees)
- An index of vegetation density (scaled 1-5, with 1 being open and 5 being almost impassable)
- Soil pH
- Distance to nearest water source; including type of water source – permanent or temporary, still or moving
- An index of leaf litter wetness (scaled 1-5 with 1 being dry and 5 being surface water)
- An indication of the surface gradient (flat, gently / moderate / steep slope)

To complement the plot searching, four drift net fence arrays were erected following the arrangement described in Heyer *et al.* (1994), with each array utilising 3 x 10” v. 4” roofing sheets and 6 x 19 or 8 litre buckets. Collars were fitted to the buckets using thick plastic sheeting. The position of these trap arrays is shown in Appendix Map 1. One further array of artificial cover traps of the type employed by Pearman *et al.* (1995), was placed on the riverbank of the Monkey Tail branch of the Raspaculo River. This was a simple 12-bucket array with each trap covered using branches and leaf litter. The traps were set at different times throughout the study periods, and once established they were left for 3 days to remove any signs of disturbance, following which they were checked daily at 9 am. Identification of specimens followed the relevant guides; Meyer & Foster (1996), Lee (1996), and Campbell (1998).

In addition to the standardised survey protocol outlined above all anecdotal recordings of these species were noted, separately, detailing the place of observation, species type and number, weather conditions, and any relevant natural history notes.

Chapter 5: Results

Table 5.1 illustrates the overall species richness found for the area around Las Cuevas, incorporating observations from both field studies as well as anecdotal notes. NB: *Scinax staufferi* was found only at Rio Frio (Caribbean Pine habitat) and never at the Las Cuevas site itself.

Table 5.1: The overall species richness of the area around Las Cuevas

Family	Species
Leptodactylidae	<i>Eleutherodactylus chac</i>
	<i>Eleutherodactylus laticeps</i>
	<i>Eleutherodactylus sandersoni</i>
	<i>Eleutherodactylus sabrinus</i>
Bufonidae	<i>Bufo campbelli</i>
	<i>Bufo marinus</i>
	<i>Bufo valliceps</i>
Ranidae	<i>Rana berlandieri</i>
	<i>Rana juliani</i>
	<i>Rana vaillanti</i>
Hylidae	<i>Agalychnis callidryas</i>
	<i>Agalychnis moreletii</i>
	<i>Hyla ebraccata</i>
	<i>Hyla microcephala</i>
	<i>Hyla picta</i>
	<i>Smilisca baudinii</i>
	<i>Smilisca cyanostica</i>
	<i>Scinax staufferi</i>
Microhylidae	<i>Gastrophryne elegans</i>
Rhinophrynidae	<i>Rhinophrynus dorsalis</i>

The results are presented separately for Field Study 1 (vocalising species) and Field Study 2 (non-vocalising species). Under Field Study 1 results are given for; (A) Species Accounts, (B) Site Accounts, and (C) a more detailed analysis of the Community Structure of the vocalising species. Weather data from the duration of our field study is presented first.

Weather

Weather data was recorded from the meteorological station at Las Cuevas, apart from between the 8th and 13th August when we were at Douglas Da' Silva Forest Station in the Mountain Pine Ridge area. Figure 5.1 gives the rainfall regime for the entire study period, showing volume of rain, hours of rain and rainfall intensity (taken as volume per hour). Figure 5.2 gives the temperature regime with respect to maximum and minimum temperatures. All weather recordings represent the 24 hour period prior to 0900 hours on the day of measurement.

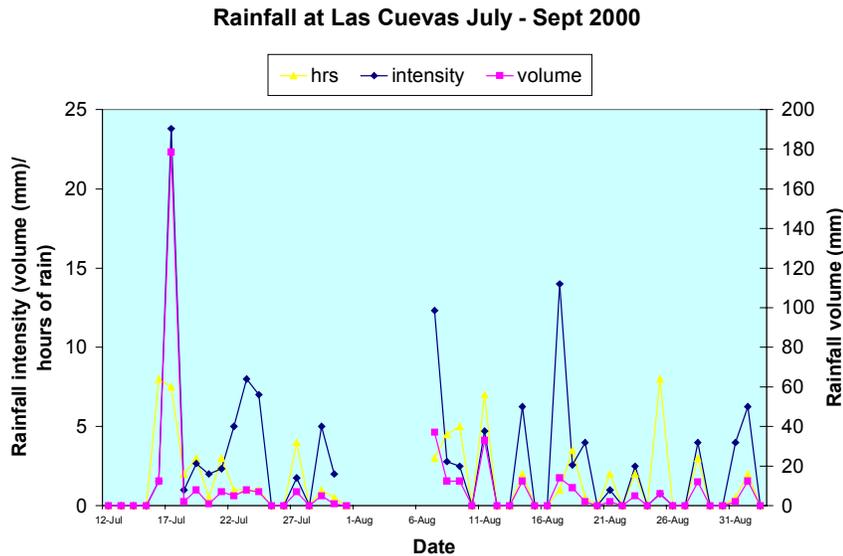


Figure 5.1: Rainfall regime during the study period

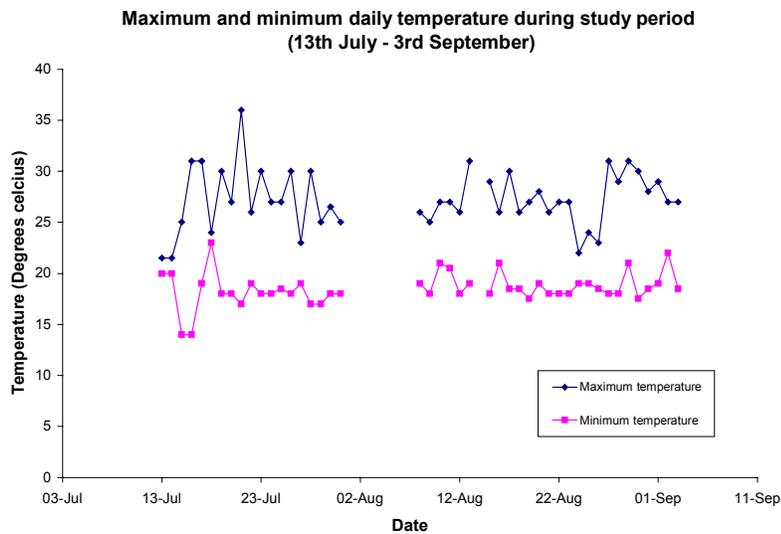


Figure 5.2: Temperature regime during the study period

Field Study 1: Vocalising species

Species accounts

A total of 9 study sites (8 at Las Cuevas and 1 at Mountain Pine Ridge) were surveyed, amounting to 25 study nights in all – including repeats. A total of 12 species of anuran were recorded during these surveys – Table 5.2:

Table 5.2: Vocalising species observed during study nights

<ul style="list-style-type: none"> • <i>Agalychnis callidryas</i> • <i>Agalychnis moreletii</i> • <i>Hyla loquax</i> • <i>Hyla ebraccata</i> • <i>Hyla picta</i> • <i>Hyla microcephala</i> 	<ul style="list-style-type: none"> • <i>Scinax stauferri</i> • <i>Bufo valliceps</i> • <i>Rana berlandieri</i> • <i>Rana vaillanti</i> * • <i>Smilisca baudinii</i> * • <i>Gastrophryne elegans</i> *
---	---

It should be noted that those species marked with an asterisk were considered to be underrepresented in the survey data with respect to both their relative abundance and calling activity. In addition to this 4 more vocalising species failed to be recorded at any of our study sites, but were recorded from anecdotal observations – Table 5.3:

Table 5.3: Vocalising species noted from anecdotal observations

<ul style="list-style-type: none"> • <i>Bufo marinus</i> • <i>Bufo campbelli</i> 	<ul style="list-style-type: none"> • <i>Smilisca cyanostica</i> • <i>Rhinophrynus dorsalis</i>
--	--

We feel that from anecdotal observations of both their abundance and reproductive activity that neither our selection of study nights and their weather conditions, or pond habitat type allowed for a fair assessment of their populations (Asterix Table 5.2, Table 5.3) in the vicinity of Las Cuevas. See Chapter (6) for further discussion of this deficiency identified in our survey methods. In light of this, a more detailed analysis of the relative abundance, calling activity and habitat associations of vocalising species is primarily made only with reference to the 9 species without the asterisk in Table 2, and to a lesser extent also including *Smilisca baudinii*.

It is instructive to first compare all species together with respect to measures of relative abundance and vocalisation activity. Following this a more detailed account of each species, including nocturnal vocalisation patterns and anecdotal observations is given. Following the data display format of MAYAMON reports (Meyer 1999a), Figure 5.3 shows a measure of relative abundance of each species across all 8 Las Cuevas study sites (Mountain Pine Ridge site is not included, and neither therefore is *Scinax staufferi*). Each species is displayed to show the number of survey nights in which it occurred and the maximum Vocalisation Category (see Chapter 4) category it attained during each of those survey nights.

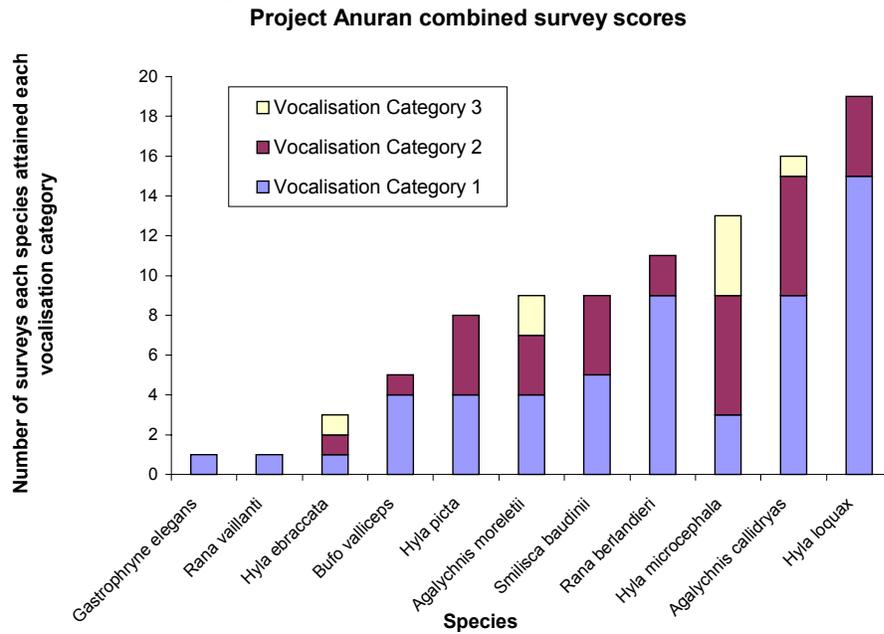


Figure 5.3: Combined survey scores of all species monitored at 8 ponds in the immediate vicinity of Las Cuevas. Each bar illustrates the number of surveys during which each Vocalisation Category was attained.

Using the available species data from all survey nights there are a great number of ways in which the population status and reproductive activity can be summarised. To avoid an exhaustive catalogue of indices and summary statistics, the salient data for each species has been summarised in Table 5.4. To allow both present and future comparisons of each species, a number of values are of interest - each of which are presented in Table 5.4;

- (1) The number of both ponds and survey nights at which each species was observed. Apart from being an index of abundance, this allows an assessment of the habitat and environmental requirements, with the more generalist species expected to be found at more breeding sites, and under a greater proportion of survey nights.
- (2) The number of hours each species was heard calling. This value is then given as a percentage of the total number of hours of recording, and secondly as a percentage only of the number of hours recorded when the species was observed to be present. The first value provides a

measure of the ‘temporal commonness’ of each species, or the extent to which one is likely to hear it during any one survey night. The second value provides more a measure of the persistence or reliability with which each species calls throughout any one night when it is seen to be active – i.e. whether the calling pattern is prolonged and continuous, or sporadic and explosive.

- (3) Summed maximum Vocalisation Category across all ponds in which the species was observed. In using an indirect measure of abundance such as Vocalisation Categories, this value is the nearest available measure to an absolute comparison of numbers of adult males of each species.
- (4) The average of the maximum Vocalisation Category observed for each species at each pond. This provides an indication of the average audible abundance (VC) of each species at any one pond at which it is observed, together with the observed level of variation.
- (5) The mean Vocalisation Category (VC) attained by each species from across all survey nights on which it was observed, accompanied by the standard error. The previous statistics use maximum Vocalisation Category values as the best estimate of the size of the breeding aggregation at each pond. To represent each species across all sites at Las Cuevas, averages are taken across ponds rather than across study nights as it is likely that the level of vocalisation observed at the same pond but on different nights is the result of the same individuals. The *mean* Vocalisation Category however, is averaged across each hour of all the study nights when the species was observed, and is therefore a measure of the *reproductive activity* of the species rather than its relative abundance. It is a measure of the proportion of which all individuals present at a pond are calling, coupled with the persistence with which they call throughout the night. The persistence with which individuals of any one species vocalise is emphasised by the fact that there is a greater proportion of zero values recorded for species which are active for a shorter period of the night. To allow for standardisation across survey nights, averages for all species are taken from 1900 to 0200.
- (6) The mean Vocalisation Intensity (VI) attained by each species from across all survey nights on which it was observed, accompanied by the standard error. Like the previous statistic this value is a measure of the reproductive activity of each species. However, rather than indicating the extent to which each species is active with respect to number of calling individuals and the duration of activity, the Vocalisation Intensity is a measure of the frequency with which any one individual of each species calls per minute. Clearly collapsing information from across all hours

in this manner obscures differences in *patterns* of reproductive activity (see below) but it does help to indicate the differences in call frequency between each species, alongside differences in high intensity calling persistence – i.e. peak callers which only briefly call at their highest frequency, whilst remaining subdued or inactive for the rest of the night, will attain a lower mean intensity level than those which reach the same level of intensity but remain highly active for much longer. It is important to note that comparisons of this nature are severely restricted by the fact that there is a high level of observer variance in determining what is a single vocalisation of any one species (see below). For example species such as *H.microcephala* call with a single distinct primary note often followed by a rapid succession of secondary notes. In a chorus of many individuals and more than one species, it can be very difficult to distinguish between separate calling individuals and thus return an accurate measure of calling intensity. To allow for standardisation across survey nights, averages for all species are taken from 1900 to 0200

- (7) Mean Vocalisation Activity (VA) attained by any one species from across all survey nights on which it was observed, accompanied by standard error. In order to describe the overall reproductive activity of any one species with respect to its average level, temporal pattern, and interactions with other species, it is useful to construct an index which incorporates the number of each species calling, and also how frequent any one individual of each species is calling. This is done simply by multiplying the Vocalisation Category by the Vocalisation Intensity for each hour the species was active. Although usually the maximum vocalisation intensity will be observed at the same time as the maximum vocalisation category, the use of the activity index allows a greater level of sensitivity in comparing the reproductive activity between species, as the range of potential values is of course greater than for either the Vocalisation Category or Intensity. To allow for standardisation across survey nights, averages for all species are taken from 1900 to 0200.
- (8) Finally; Number of anecdotal observations. Every time an individual of each species was observed in the field but outside of a standard survey night, it was recorded. Although such recordings are highly biased due to variance in observer vigilance and distribution they do serve to identify inadequacies in our technique, in that some clearly abundant species are severely underrepresented in the official record.

A (ii). Individual species accounts

In order to summarise the information presented in Table 5.4 in the context of each species, it is instructive to treat each species separately with respect to its relative abundance and calling activity. For consideration of habitat and environmental associations of each species see below; Site Accounts, and Community Structure.

1. *Bufo valliceps* (Gulf Coast Toad)

Bufo valliceps was heard on only 20% of survey nights and at 2 pond sites. A consequence of this was that it was only heard for a total of 18 hours or 24% of the total recorded time. From the survey data the index of total number of males observed across all study sites was 15.5, with the average Vocalisation Category only reaching 1.3 (+/- 0.58) indicating that it was rarely seen in numbers greater than 5 (maximum of Vocalisation Category 1). All this information suggests a low level of abundance alongside a restricted distribution – both geographically across pond sites, and temporally across study nights. However, as is clear from the anecdotal records (>250 observations), this conclusion represents a deficiency in the survey method (see below). This deficiency is not, however, surprising as *B.valliceps* is known to be what is termed an ‘explosive’ breeder (Wells 1977), associated with marked spatial clumping around suitable oviposition sites, and often requiring a climatic stimulus to be active (e.g. intense rain). During periods of intense rainfall or tropical storms, a great number of *B.valliceps* would congregate in open areas, namely tyre tracks on the main paths into and out of the research station, in addition to the main helicopter clearing. This rather sporadic calling behaviour is clearly reflected in the mean vocalisation statistics, which are all relatively low in comparison to other species, emphasising that not only was *B.valliceps* rarely observed on study nights, it also remained largely inactive during the recording.

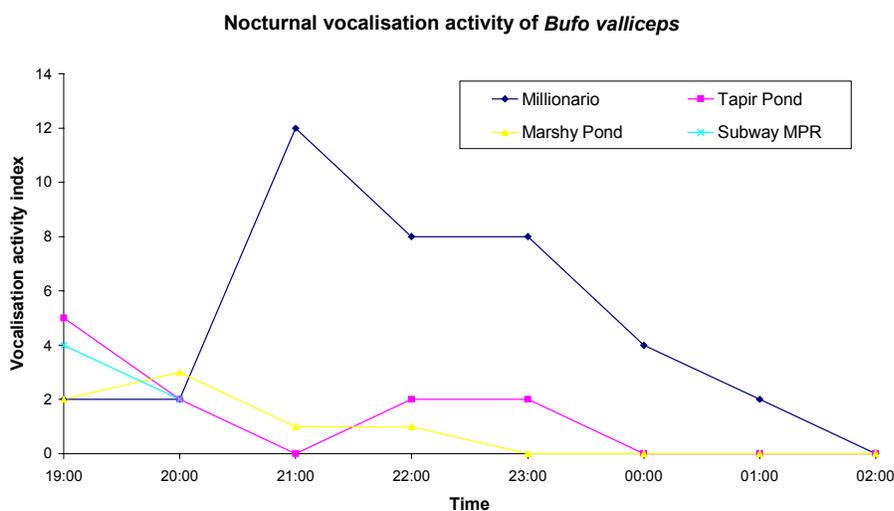


Figure 5.4: Nocturnal vocalisation activity (index) of *Bufo valliceps* across all pond sites at which it was observed.

Species	Number of Las Cuevas pond sites observed in	Total number of survey nights recorded (value in brackets as a % of maximum – 25 nights)	Total number of hours heard calling	Number of hours heard calling as a % of absolute maximum hours recorded across all study nights – 175 hours	Number of hours heard calling as a % total number of hours recorded on nights when the species was present	Summed maximum Vocalisation from Category across all ponds in which the species was observed	Maximum Vocalisation Category averaged across all ponds in which the species was observed. Calculated using mid-point values for each VC (+/- SE)		Mean Vocalisation Category attained in any one night when present (+/- SE)		Mean Vocalisation intensity attained in any one night when present (+/- SE)		Mean Vocalisation activity (index) attained in any one night when present (+/- SE)		Number of anecdotal observations
							Mean	SE	Mean	SE	Mean	SE	Mean	SE	
<i>Bufo valliceps</i>	3	5 (22)	18	24	35	15.5	1.3	0.58	0.593	0.21	1.406	0.50	1.843	0.90	>250
<i>Agalychnis callidryas</i>	6	17 (74)	109	62	76	79.5	1.83	0.75	0.963	0.09	2.213	0.39	2.661	0.56	1
<i>Agalychnis Moreletii</i>	3	9 (39)	69	39	96	84	2.6	0.58	1.306	0.14	3.25	0.37	5.028	1.12	1
<i>Hyla loquax</i>	7	19 (82)	89	51	59	49	1.43	0.53	0.651	0.10	2.213	0.39	2.661	0.56	>30 and <50
<i>Hyla picta</i>	3	9 (39)	42	24	58	39	2	0	0.768	0.15	2.843	0.69	3.522	0.10	0
<i>Hyla microcephala</i>	5	12 (52)	75	43	78	110	2.4	0.55	1.10	0.15	3.035	0.43	5.200	0.88	5
<i>Hyla ebraccata</i>	1	3 (13)	13	7.4	88	35.5	3	0	1.292	0.34	3.542	0.71	6.042	1.99	0
<i>Gastrophryne elegans</i>	1	1 (4)	3	0.02	38	2.5	1	0	0.375		0.875		0.875		>10 and <20
<i>Smilisca baudinii</i>	5	9 (39)	34	19	47	12.5	1	0	0.458	0.10	0.854	0.23	0.792	0.23	>250
<i>Rana berlandieri</i>	4	13 (56)	57	33	65	20.5	1.25	0.5	0.514	0.12	1.40	0.47	1.125	0.39	5

Table 5.4: Summary relative abundance and vocalisation activity data from across 23 study nights and 10 species. Note that data from Subway MPR is not included, as the Table serves to describe the status and behavior of anurans in the region around Las Cuevas only. Consequently data on *Scinax staufferi* is not included here.

Figure 5.4 illustrates the *pattern* of nocturnal vocalisation activity for *Bufo valliceps* across all pond sites at which it was observed. A lack of repeat observations at any one pond precludes the inclusion of standard error bars for each hour of calling. However, it can be clearly seen that there is no distinct peak in calling activity, and no obvious congruence between patterns observed at different sites.

2. *Agalychnis callidryas* (Red-eyed tree frog)

Agalychnis callidryas was observed at 6 out of the 8 Las Cuevas study sites and on 17 study nights. In keeping with such a widespread presence across both the majority of habitats and the majority of study nights (climatic conditions), it was heard for 62% of the total recorded time during the entire study period – and in this regard was the most prevalent species found at Las Cuevas. The clear persistence in the nocturnal vocalisation activity of this species is further emphasised by only considering the study nights on which it was active - when it was observed to call for 76% of the recorded time. The index of the maximum number of males observed across all sites indicates that it was the third most abundant species to be recorded in this manner, with a value of 79.5, although this is largely due to the fact that it was observed in relatively low numbers but at many sites, as the average maximum Vocalisation Category was only the fifth highest value out of the ten species compared, being at 1.83 (+/- 0.75). The persistence of its calling activity indicated by the high percentage of hours heard is further shown by the relatively high mean vocalisation indices across all survey nights – both for audible abundance (VC), and calling activity (VA). However, as noted above these indices attain their high value largely due to their high level of persistence (and therefore few hours of complete inactivity), rather than being either at a high level of local abundance or calling activity on any one survey night. Figure 5.5 shows the temporal pattern of vocalisation activity for *Agalychnis callidryas*, across all 6 sites at which it was observed. Standard error bars illustrate the variance in activity at each hour from across survey repeats for each pond. It is interesting to note that contrary to *B.valliceps* the pattern of vocalisation activity shows a considerable degree of congruence across different sites – this is especially evident in comparing Puzzle Pond and the Aguada. Owing to its rather discrete, arboreal nature, only a single *Agalychnis callidryas* individual was observed anecdotally outside an ‘official’ survey night. This suggests that one can attribute far more confidence to the summary statistics presented above as being representative for the species, in comparison to a typical explosive breeder such as *B.valliceps*. However, it must be noted that such confidence is only in reference to the relative values and indices – the behaviour of these species, the

complexity of the terrain, and the high level of observer bias preclude concluding any *absolute* statistics.

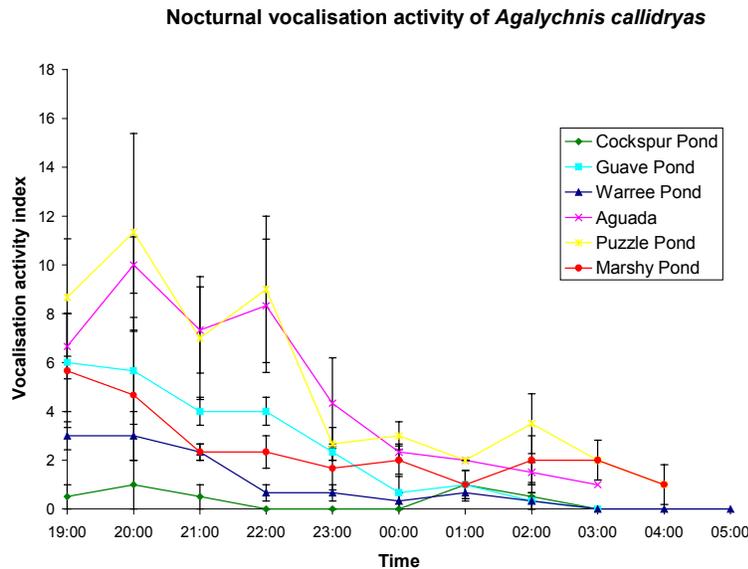


Figure 5.5: Nocturnal vocalisation activity (index) of *Agalychnis callidryas* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

3. ***Agalychnis moreletii* (Morelets tree frog)** *Agalychnis moreletii* was observed at only 3 of the Las Cuevas study sites, and a total of 9 survey nights (comprising every study repeat of these same sites). These figures, alongside it being recorded for only 39% of the total recorded study period, suggest that it is far less prevalent than its close relative *Agalychnis callidryas*. Whether this is due to a limiting requirement for the abiotic and biotic factors which describe the habitat type of sites where it was found, or rather due to limiting biotic interactions with other species (i.e. competition, predation) is unclear. However, the fact that it was found on *all* study repeats of the three sites suggest that its absence from other survey nights was not due to coincidental weather conditions, but rather some characteristic feature of these sites, be it either biotic or abiotic. The importance of considering the number of hours each species was active separately with respect to total recorded time and total recorded time for active nights only, is emphasised by the fact that although *A. moreletii* is heard for a relatively small proportion of the total recorded time, it was recorded for 96% of the time during which it was observed to be active. The index of the maximum number of males observed across all sites indicates that it was the second most abundant species to be recorded in this manner, with a value of 84 individuals. Contrary to *A. callidryas*, *A. moreletii* is also shown to be at a high relative abundance at each of the sites where it was found, with an average maximum VC of 2.6 - the second highest value of this index. The description of this species being both highly evident but also quite strictly localised is further

shown by it having the highest mean VC from across all study nights – illustrating a high level of persistence in its nocturnal vocalising activity with relatively few periods of complete inactivity. Furthermore, and again in contrast to *A.callidryas*, the intensity of its vocalisation rate places it as one of the most active species, with the mean VI being the second highest value (3.25) alongside the third highest mean VA (5.03). In summary it can be seen that *A.moreletii* presents a very different pattern of distribution and reproductive activity to that of *A.callidryas*, with the former being found in far fewer sites, but at a higher relative abundance, and exhibiting a higher average level of vocalisation activity. Figure 5.6 shows that *A.moreletii* also shows a close degree of congruence between sites in its vocalisation activity. As for *A.callidryas* it can be seen that *A.moreletii* peaks in its activity early in the evening (around 2100) although there is a high level of variation across study nights, especially during the peak of activity. It is also interesting to note from Figure 5.6 that a dawn chorus can be observed in *A.moreletii* at around 0400, although the

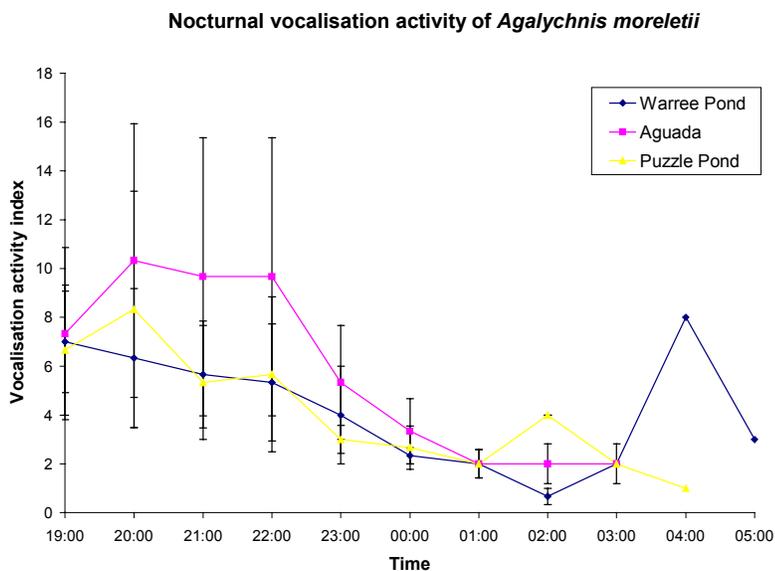


Figure 5.6: Nocturnal vocalisation activity (index) of *Agalychnis moreletii* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

ecological significance of this is far from clear. As for *A.callidryas*, it can be seen from Table 4 that only a single *A.moreletii* individual was observed outside of an official survey night.

4. *Hyla loquax* (Loquacious tree frog)

Hyla loquax was observed at 7 out of the 8 Las Cuevas study sites and on 19 (or 82%) of study nights. In this respect it can be regarded as the most widely occurring species found at Las Cuevas, both with respect to habitat type, and with respect to variance in climatic conditions. The common appearance of the species is also upheld in that it was observed for 51% of all recorded time, although this was less than *A.callidryas* which was observed at both fewer sites and on fewer nights.

Despite this apparent prevalence it was shown to be a much less persistent in its vocalisation activity throughout any one survey night than many other species, with it calling for only 59% of the total time for all its active nights – the 6th highest value (see Table 5.4). Although this relatively low level of temporal persistence in the reproductive activity of the species may be largely due to characteristics of its calling behaviour, it is at least partly due to its relatively low level of abundance in the Las Cuevas area, with the index of maximum number of males being the 4th value at 49 individuals, and the average maximum VC being the 6th value at 1.43 (+/- 0.53). The rather sporadic nature of its vocalisation activity on any one active night is further shown by the relatively low mean vocalisation indices, both with respect to the audible abundance (VC) and calling intensity (VI). It is important to emphasise here that the value of any mean vocalisation index is the product of both the number of individuals present, and the temporal pattern of vocalisation activity particular that species. It is therefore often difficult to identify whether a low mean value is due to few individuals or an infrequent calling pattern (although some insight can be gained from the average maximum VC, and % hours calling when active). One determinant of this is whether inter-specific competition for uninterrupted calling time is stronger than potential intra-specific competition. If the former is true, as is held for many species (Wells 1977; Rand & Myers 1990), then there would be strong selection pressure for all individuals of one species to call in synchrony in order to avoid acoustic interference from other species. A low value for a mean vocalisation category or activity index would therefore represent a weakly persistent or rather sporadic calling behaviour of the species rather than simply few individuals per se (the average value being weighted by periods of inactivity of all individuals). Although many species have been noted to display a remarkable synchrony in calling patterns little is known about the nature of the stimuli which precipitate the start and finish of any one particular chorus (Wells 1977; Schwartz & Wells 1985). Figure 7 shows the temporal pattern of vocalisation activity for *H.loquax* across all 7 sites at which it was observed. An early peak in calling activity can be seen from across all ponds, and a quite remarkable degree of congruence in both the pattern of vocalisation activity and the degree of variance across study repeats can be seen between Millionario and Guave Pond.

5. *Hyla picta* (Painted tree frog)

Hyla picta was observed at only 3 sites at Las Cuevas and on a total of 9 study nights. Despite the fact that this represents the same degree of commonness across both different sites and different nights as *A.moreletii*, *H.picta* was both heard far less frequently and at lower levels of relative

abundance. This is illustrated by the fact that it was only observed for 24% of all recorded time, and attained the fifth index value for the maximum number of males at 39 individuals, and the 4th value for the average maximum VC at 2.

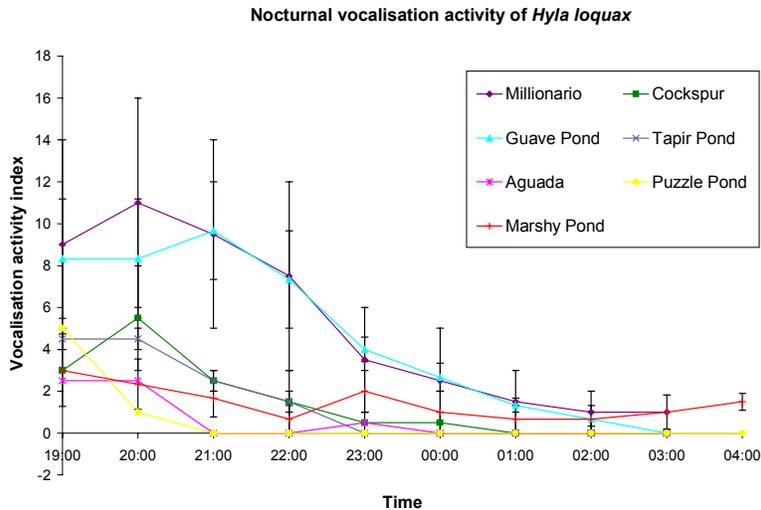


Figure 5.7: Nocturnal vocalisation activity (index) of *Hyla loquax* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

In further comparison to *A.moreletii*, *H.picta* is shown to be far less persistent in its vocalisation activity during any one active night, with the value for the percentage of hours active on observed nights being 58% - almost half that of *A.moreletii* but almost identical to that of *H.loquax*. As was noted above there is a significant potential for error in reporting either the VC or VI of species with different call characteristics, with an equal degree of reliability. This is particularly relevant for *H.picta* which has a relatively indistinct call in comparison to many of its sympatric species, and could easily be underrepresented by the observer in both number and call frequency when calling from within a large chorus. In contrast *A.moreletii* never called from within a large chorus of more than 3 species, and exhibits a very distinct and easily distinguished vocalisation. Both the relatively low abundance and infrequent calling pattern combine to produce a relatively low mean vocalisation index. However, the mean VI is comparatively high in comparison to the level of abundance, indicating that when it does call it is often at a relatively high frequency – although once again this measure is biased by the unavoidable subjectivity in defining a distinct vocalisation, especially as *H.picta* calls in a quick succession of notes, the separation of which can be very difficult when in a chorus. Figure 5.8 shows the temporal pattern of nocturnal vocalisation activity for *H.picta* across all sites at which it was observed. Aside from the values from Cockspur pond the activity of *H.picta* at the three other ponds shows a remarkable degree of congruence in both the overall temporal pattern, and the timing of peak vocalisation activity. Some explanation for the difference observed

at Cockspur pond is that this is the only site at which only 2 survey repeats were conducted, in contrast to the other three whose mean values are taken from the standard 3 repeats.

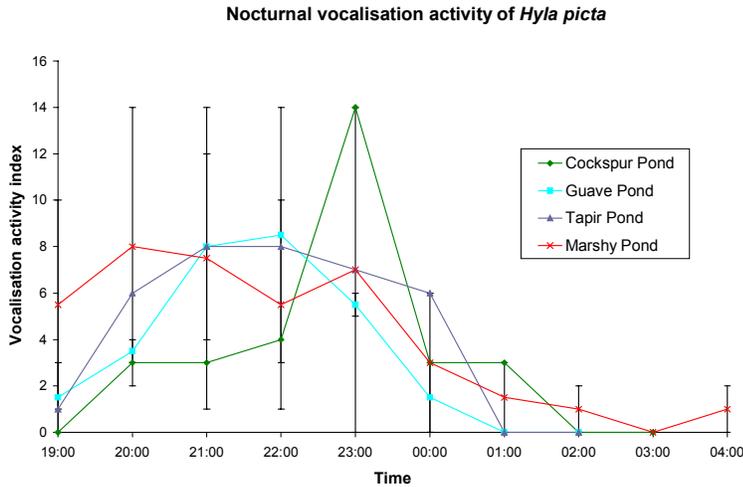


Figure 5.8: Nocturnal vocalisation activity (index) of *Hyla picta* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

6. *Hyla microcephala* (Small-headed tree frog)

Hyla microcephala was observed at 5 of the 8 Las Cuevas study sites, and on just over half the total number of study nights, indicating it to be a reasonably common species. Aside from its relatively widespread presence across different ponds and different nights, it is further apparent to the casual observer due to its high level of vocalisation activity – being heard on some 43% of the total recorded time (the 3rd highest value for this index). Unsurprisingly this value is much higher (78%) when considered only across nights when *H.microcephala* was active, indicating a relatively ‘complete’ use of the available time for nocturnal vocalisation activity. The fact that it was found across a relatively high number of sites (63%), coupled with a high maximum vocalisation category at any one site (2.4 +/- 0.55), means that with respect to the index of the maximum number of males observed, it was seen to be the most prevalent species, with a value of 110 individuals. This means that as well as being almost as widespread as *A.callidryas* and *H.loquax*, when it did occur it was found in persistently higher numbers than either of these other two relatively common species. The appearance of large choruses of calling males of this species during the wet season is a recognised phenomenon, although it is thought to be far less common in undisturbed habitats such as that around Las Cuevas, than in disturbed areas near settlements (Lee 1996). The appearance of relatively higher numbers of this species in comparison to say *A.callidryas* can largely be attributed to the very obvious fact that it is simply much smaller, rather than any more subtle ecological differences in habitat or climatic suitability of survey night conditions. The relationship between mass and relative abundance is thought to be one of the few underlying ‘laws’ in ecology, due to

reasons of resource partitioning and finite niche space (Rosenzweig 1995; Lawton 1999). As well as the high percentage of hours in which *H.microcephala* was heard calling, its high level of reproductive activity is further emphasised by the high mean VC, VI and VA indices, with the latter being the second highest level of vocalisation activity across all ten species – an observation which is due both to its relatively high numbers and persistent calling behaviour. It is pertinent to note here another important caveat in using measures of audible abundance to assess relative abundance. This is the fact that many species, and in particular *H.microcephala* call not only for the purposes of mate attraction but also in response to the aggressive or territorial calls of other males (Schwartz & Wells 1985 – see below). Although to the experienced observer this should not alter the level of VC recorded, it can make accurate recording much more difficult from within a large chorus. Furthermore the observed level and pattern of calling activity may be less a product of direct inter-specific and historical competition for uninterrupted calling ‘space’, and more a product of the number of conspecific males which were present during the particular study night.

Figure 5.9 shows the pattern of nocturnal vocalisation activity for *H.microcephala*, across 4 sites at which it was observed. Although it was observed at Tapir Pond, it was only heard for 1 hour and as such is not included in this picture. Out of all 10 species summarised in Table 5.4, and that were recorded during Field Study 1, *H.microcephala* demonstrates the highest degree of congruence in calling pattern, timing of peak activity, and hourly variance across site repeats, from all species. See below for discussion of temporal patterns of vocalisation activity.

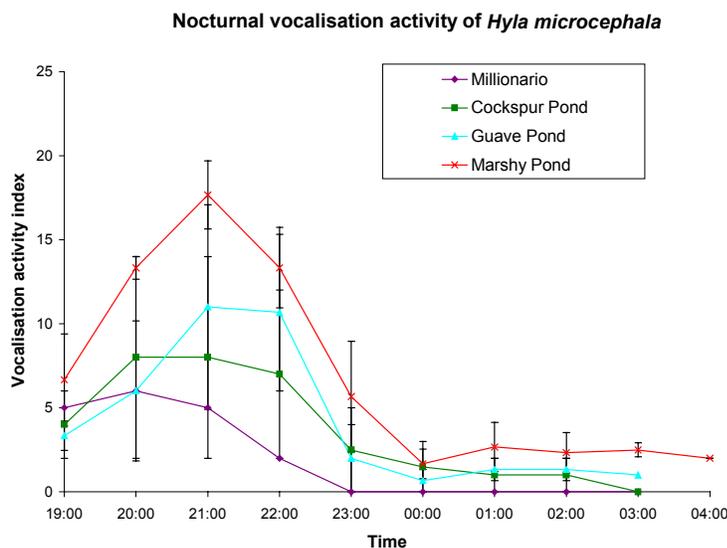


Figure 5.9: Nocturnal vocalisation activity (index) of *Hyla microcephala* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

7. *Hyla ebraccata* (Hourglass tree frog)

Hyla ebraccata was found at only one single site (Marshy Pond), although it was active for all three survey night repeats. Since our selection of study sites was made with a great deal of subjectivity (e.g. ease of access, requirement to be filled during study period), it is unclear as to whether this geographic restriction is a product of either the ecological suitability of Marshy Pond, or some biotic or abiotic environmental restriction of all other study sites, or rather purely a chance product of the limited complement of our study sites. Despite this restriction to only one site, *Hyla ebraccata* was observed to be both relatively abundant and highly active on all nights during which it was observed. This is indicated by the fact that it was heard on 88% of all recorded time at Marshy Pond (second only to *A.moreletii* in calling persistence), and was found persistently at Vocalisation Category 3, giving it the maximum mean VC across all species. However, due to its restricted geographic distribution *H.ebraccata* has one of the lowest overall levels of relative abundance with respect to the index of maximum number of males which was the sixth value at 35.5. With respect to levels of vocalisation activity and in light of both its localised distribution, high local abundance and persistent calling pattern, it exhibits the highest mean Vocalisation Activity at 6.04, in addition to the second highest mean Vocalisation Category at 1.29 – thus emphasising that most individuals were active at a relatively high level of intensity, for a significant proportion of the time between 1900 and 0200. It is relevant to note that as for *H.microcephala* the rather indistinct nature *H.ebraccata*'s vocalisation precludes a high level of confidence in recording its level of vocalisation activity. This difficulty is further exacerbated by the fact that *H.ebraccata* males call aggressively both in response to conspecifics (Wells & Schwartz 1984), but also in response to calls of *H.microcephala* males, whose vocal repertoires are functionally and structurally very similar (Schwartz & Wells 1985). It can be seen from Figure 5.10 that this similarity in call pattern is reflected in the congruence between the temporal pattern and timing of peak activity shown for *H.microcephala* in Figure 5.9, although the variance in mean vocalisation activity during any one hour is noticeably greater for *H.ebraccata* (Figure 5.10).

8. *Gastrophryne elegans* (Elegant narrowmouth frog)

Gastrophryne elegans was observed only at 1 study site (Marshy Pond as for *H.ebraccata*), but also only for one study night, and furthermore for only 3 hours. However, as was noted above, this species was considered to be underrepresented using this method of monitoring. Justification for this comes from the anecdotal observations of perhaps more than 20 individuals in the main station

clearing during a storm on the 3rd September. This observation suggests that as for *B.valliceps*, *Gastrophryne elegans* is an explosive breeder (Wells 1977), and as such is particularly difficult to assess using conventional scheduled monitoring procedures (see below). The lack of any repeat recordings of either the local relative abundance or calling activity of *G.elegans* precludes affording any real confidence to the indices presented in Table 5.4.

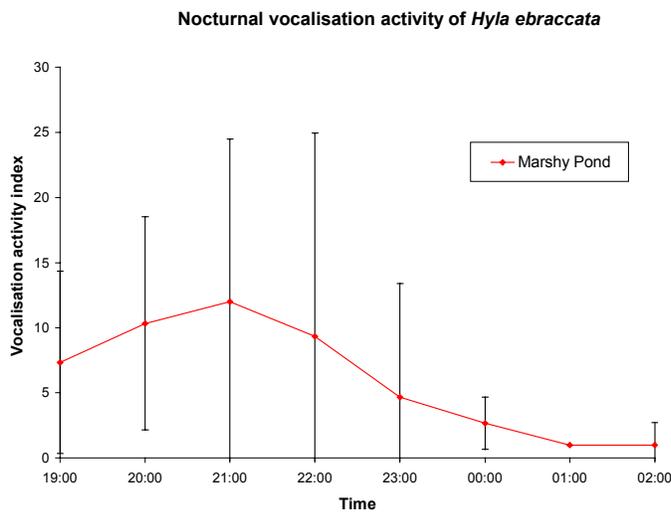


Figure 5.10: Nocturnal vocalisation activity (index) of *Hyla ebraccata* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

9. *Smilisca baudinii* (Mexican tree – frog)

Smilisca baudinii was observed at 5 study sites, but only on 9 different study nights. This immediately indicates a significant discrepancy to many of the above species, in that although it appears to show little in the way of specialist habitat requirements (being geographically widespread), its infrequent *temporal* occurrence suggests a reliance on particular climatic conditions to stimulate vocalisation activity. This fact is further emphasised by its observation during only 19% of all recorded time, and even during nights when it was observed to be active it was recorded for only 47% of the time – the third lowest value after *B.valliceps* and *G.elegans*. Unsurprisingly therefore, *S.baudinii* also exhibited one of the lowest levels of total male abundance at 12.5 individuals, explained by the fact that the average maximum VC was 1 with zero level of variance – signifying it was never observed in numbers greater than 5 during any study night. In keeping with the clearly sporadic appearance of this species, the mean vocalisation indices are characteristically very low, emphasising both very low numbers, and a highly infrequent calling behaviour, interspersed by prolonged periods of complete inactivity. In light of these observations, Figure 5.11 shows the expected lack of congruence between the patterns of vocalisation activity for *S.baudinii* across the different ponds at which it was observed. Unlike many of the above species which appear to show strong tendencies towards a

consistent peak in calling time *irrespective* of the site or climatic conditions (perhaps therefore a product of stabilising selection due to interspecific competition), *S.baudinii* exhibits a seemingly stochastic pattern of reproductive activity, suggesting the role of temporally variable environmental stimuli in precipitating chorusing. This theory is supported by anecdotal observations, which recorded more than 250 individuals – almost exclusively due to the observation of mass breeding congregations during intense periods of rainfall or tropical storms. As for *G.elegans* and *B.valliceps* it is once more clearly evident that the adopted MAYAMON protocol is severely deficient in accurately assessing the relative abundance of typically explosive breeders such as *S.baudinii*.

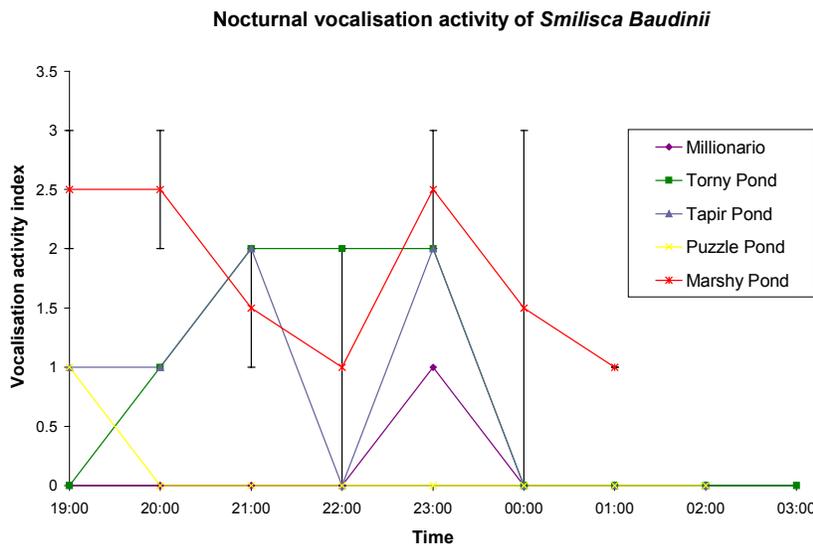


Figure 5.11: Nocturnal vocalisation activity (index) of *Smilisca baudinii* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site.

10. *Rana berlandieri* (Leopard frog)

Rana berlandieri was observed at half of the 8 study sites at Las Cuevas, and on just over half of the total number of study nights, both of which measures indicate that it was moderately common across both different habitat types and different climatic conditions (study nights). With respect to number of hours called both as a percentage of the total recorded time, and of only the nights when active, it also ranked midway with respect to the other 9 species monitored during Field Study 1. However, although it was seen on a relatively high number of nights, in addition to exhibiting a high degree of calling persistence during any one active night (recorded for 67% of active time), it was never observed in high numbers. The index of the maximum number of males across the area was the 4th lowest value after the 3 explosive breeders (see above), and the average maximum VC was the 3rd lowest value at 1.25, with no one study night recording a total abundance of more than category 2 (20 individuals). Aside from being present in relatively low densities, *R.berlandieri* also showed a low value for the mean vocalisation indices, which despite a relatively persistent calling pattern, is the

product of both low numbers, but also a low intensity of calling rate. The comparative nature of this index of calling rate between different species is again identified as being of limited reliability. The call of *R.berlandieri* is not one distinct vocalisation as is true for the *Agalychnis* species, but rather a complex series of trills and grunts (Lee 1996), which can often be difficult to distinguish between different males in a chorus. Figure 5.12 shows the temporal pattern of vocalisation activity for *Rana berlandieri*, across all 5 sites at which it was observed. A measure of variance in the activity observed each hour across different study repeats at the same site is only available for Guave Pond, as *R.berlandieri* was only observed during a single visit at all other sites – an observation which perhaps suggests the importance of varying climatic characteristics in precipitating calling for this species. Despite significant variance in vocalisation activity during the early part of the night, it is clear that the peak of activity is much later than many other species detailed above, being much closer to midnight – an observation which has been previously noted (Blair 1961).

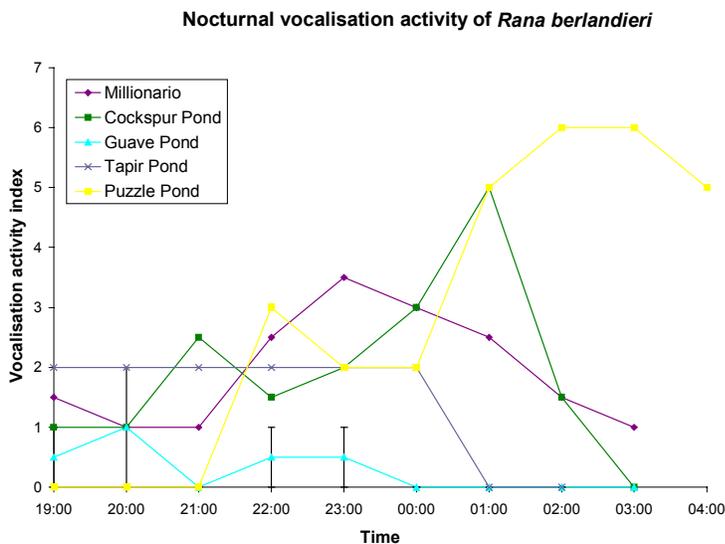


Figure 5.12: Nocturnal vocalisation activity (index) of *Rana berlandieri* across all pond sites at which it was observed. Also shown are standard error bars taken from the survey night repeats for each site (where available).

As indicated above a number of additional vocalising species that were observed to be present at Las Cuevas were not recorded during any survey nights. It is instructive to provide a brief anecdotal description as to their status around Las Cuevas, and an indication as to why they failed to be recorded under the standard monitoring program.

- a) ***Rana vaillanti* (Rainforest frog)** Although as indicated in Table 2, *Rana vaillanti* was observed during a survey night (Tapir Pond), this represented a single and unconfirmed sighting, precluding any level of analysis as detailed above for the other species. Following this a number

of anecdotal observations were made, the majority of which were at both the Monkey Tail and Rio Frio rivers, although two individuals were found in the main clearing at Las Cuevas. It is possible that this species was present on a number of our study nights, but that it either remained inactive, or that its rather quiet and indistinct call obscured its presence in a multi-species chorus. It is interesting to note that Lee (1996) sites *R.vaillanti* as not known to co-occur with *R.juliani* – the Maya Mountain endemic. However, the anecdotal sightings of *R.vaillanti* at the Rio Frio river in the Mountain Pine Ridge area were twice accompanied by sightings of *R.juliani* individuals in the immediate vicinity – one of many observations which serve to highlight the lack of understanding of the ecology of many of the species in Table 1.

- b) ***Bufo campbelli* (Campbell's Forest Toad)** As this species was only recently discovered, the extent of its distribution and natural level of abundance is largely unknown. We were therefore quite pleasantly surprised to record at least 20 sightings of individuals. Interestingly all anecdotal recordings for this species were on a small length of the main track to the Monkey Tail River, about 500 m from the river itself. An intriguing feature of this section of track is that it is made up of dark red clay – not at all dissimilar to the characteristic rust coloured blotches that are often found on the dorsal surfaces of *B.campbelli*, prompting the suggestion that the blotches were a result of local selection pressure to avoid predation! Although our nearest study site to this area was the Aguada, about 1.5 miles towards the research station, it was possible that a number of vocalising *B.campbelli* individuals were wrongly recorded as *B.valliceps* – the vocalisations of each species having remarkably similar acoustic characteristics (Lee 2000).
- c) ***Bufo marinus* (Marine Toad)** Although there was no confirmed hearing of this species calling during the entire study period, at least 3 individuals were found on the banks of the Monkey Tail River. It seems likely that the limitation of our study sites to relatively small breeding ponds was the main reason behind its absence from all surveys. However, it has been recognised that the availability of suitable terrestrial habitat and diurnal shelter sites are critical to the existence of this and many other species (Stewart & Pough 1983; Schwarzkopf & Alford 1996). Although the micro-environmental conditions around Las Cuevas are highly varied (Furley *et al.* 2000), it is possible that the majority of environmental conditions and vegetation type are largely unsuitable for *B.marinus*. As has been noted by a number of authors (Lee 1996; Meyer & Foster 1996; Lee 2000), *B.marinus* is frequently observed in disturbed habitat, an characteristic that was upheld by our own sightings in many of the kitchens and bars of San Ignacio !

- d) ***Smilisca cyanostica* (Blue-spotted tree frog)**. Although this species was never recorded during an official survey night it appeared to be a relatively abundant member of the amphibian community around Las Cuevas. This conclusion comes from two notable and distinct sightings. The first was during the acclimatisation week at the start of July, when at least 10 individuals were sighted at Warree Pond, where they were seen to be actively calling for three consecutive nights. However, after this their presence was not seen again at Warree pond despite many repeated visits. It seemed of relevance that whilst *S.cyanostica* was active neither of the *Agalychnis* species which were found to be relatively common there later, were neither heard nor seen. In light of the acoustically similar nature of the vocalisation of *S.cyanostica* to both *Agalychnis* species (see Project Anuran CD), we felt that this temporal partitioning of calling activity through the wet season, could be a result of negative inter-specific interactions due to either competition for free calling time, or confusion in caller identity by females leading to inefficient vocalising by the males of either species. Throughout all of July and most of August no further sightings of *S.cyanostica* were made until a period of 5 days between 22nd – 25th August when more than 25 individuals were sighted – all in tyre tracks and temporary standing water on the main track between Las Cuevas and Monkey Tail river. The reason behind either their apparent disappearance for the interim period between the two sightings, or the sudden resurgence in activity is unclear, although the much of July and August were noted to be uncharacteristically dry during 2000 (N. Bol pers. comm.)
- e) ***Rhinophrynus dorsalis* (Mexican Burrowing Toad)**. This species is a classic example of what Wells (1977) terms an explosive breeder, congregating in large groups to breed, and only during periods of heavy rain or tropical storms (Lee 1996). In keeping with this and the sporadic appearance and vocalisation activity of the other rather explosive breeders noted above (*B.valliceps*, *S.baudinii*, and to a lesser extent, *G.elegans*), *R.dorsalis* was only observed on a number of distinct occasions during heavy periods of rainfall. However, at each observation a considerable number (>250) individuals could be both heard and seen, most obviously in large breeding congregations directly in front of the research station. As for a number of other species it was impossible to conduct a reliable assessment of *R.dorsalis* using the standard protocol.

The final addition with respect to species accounts, is *Scinax staufferi* or Stauffer's tree frog, which although was not observed in the vicinity of Las Cuevas, was noted to be particularly abundant at

the Subway MPR site in the Mountain Pine Ridge region (see Site Accounts). It is not clear whether its presence here and absence at Las Cuevas is due to a lack of sensitivity in our survey regime, a chance colonisation event at MPR, or local environmental characteristics of both or either sites. It is interesting to note however, that Lee (1996) remarks that it is thought to avoid deep forest, of which Las Cuevas is a typical example, rather preferring open areas, often within or near to savanna (MPR is a type of savanna; P.A. Furley pers. comm.). Although in the context of the amphibian community at Las Cuevas no analytical comparison between species abundance and vocalisation activity similar to that in Table 5.4 can be conducted, it is of interest to present the *pattern* of vocalisation activity of *S.staufferi*. This is of use as not only does *S.staufferi* live sympatrically in other areas with many of the hylid species found at Las Cuevas (Lee 1996), it is found at a number of other MAYAMON study sites throughout the Yucatan, and an appreciation as to its pattern of reproductive behaviour is useful for the construction of efficient monitoring programs. Figure 5.13 shows the temporal pattern of vocalisation activity for *S.staufferi* observed across two repeat surveys at the Subway MPR site. Although there is a high degree of variance both at the start and end of the evening, it is interesting to note that the high peak of vocalisation activity forms a plateau for 2-4 hours – in contrast to the more defined peaks of many other species such as *H.microcephala* or *H.picta*.

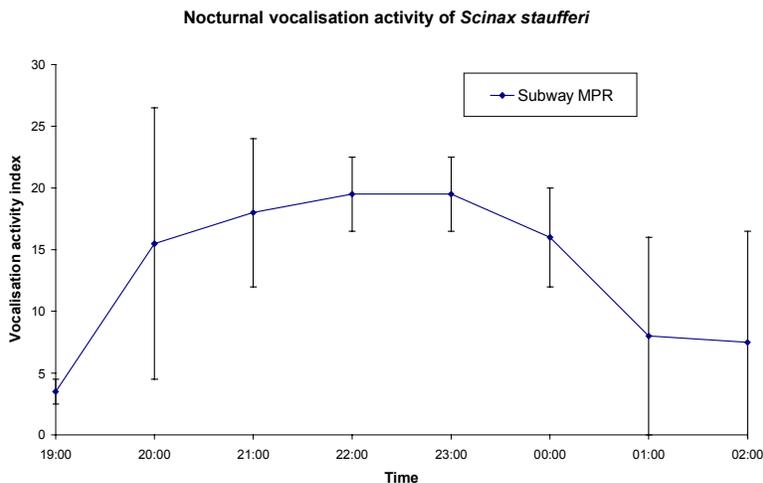


Figure 5.13: Nocturnal vocalisation activity (index) of *Scinax staufferi* at Subway MPR site. Hourly vocalisation activity values are taken from across the two survey nights.

Site Accounts

A total of 8 study sites were surveyed in the area around Las Cuevas, in addition to one site in the Mountain Pine Ridge area. The distribution of all study sites in the Las Cuevas area is shown on the site map in Appendix 1. In this section, each study site is described in turn with respect to its physical characteristics, the species composition, relative abundances and temporal vocalisation activity patterns. There are a number of important justifications for considering the status and activity of each species with respect to *between* site comparisons, in addition to *across* site comparisons (see Species Accounts). As noted in Chapter 1, amphibians are frequently considered to display a metapopulation structure, indicating that an understanding of the variability in the spatial population dynamics of each species is critical in considering its long-term stability (Marsh & Trenham 2000). In order to distinguish local, and essentially stochastic extinctions which are an inherent part of the overall dynamics of many amphibian populations, from more worrying regional declines, it is necessary to have a regional monitoring perspective, encompassing both a number of different breeding sites and populations. In monitoring 8 different sites, we are afforded the opportunity in future years to compare the local fluctuations in assemblage composition and vocalisation activity at any one pond, with fluctuations of the same species at a much broader spatial scale – one of the main challenges facing biologists studying the declining amphibian phenomenon (Alford & Richards 1999; Marsh & Trenham 2000). Aside from identifying population declines, an appreciation of the contribution of local (site) extinctions to the regional population dynamics of an amphibian is important in being able to elucidate the potential role or contribution of local environmental changes (both in physical characteristics and biotic interactions) to regional population declines. It is therefore instructive to report the analogous statistics for each species presented in Table 5.4, with respect to each individual *pond* in turn. Furthermore, in comparing the influence of local biotic (amphibian assemblage composition, local predators, floral composition) and abiotic (physical pond attributes, chemical qualities) environmental features particular to each pond, against the influence of more regional features (regional species composition, vegetation type, climatic zone etc), on the temporal vocalisation pattern of each species, it is necessary to present the analogous pictures to Figures 5.4-5.12 for each pond in turn.

Each site is described below with respect to its species diversity, summary population and reproductive activity statistics, and physical environmental attributes. A map detailing the location,

size, depth, and local tree species composition of each site is given in Appendix 2. Further measurements that were taken at each pond for every survey night are given in the raw data sheets in Appendix 3. Where available, a photograph is provided of each pond on Plate 5.

Table 5.5 summarises the number and type of each species found at each site, in addition to the number of site survey repeats in which each species occurred (out of a maximum of 3). Aside from providing a useful overview, Table 5.5 indicates the number of values (1,2 or 3) that each hourly data points was calculated from on both the species and site nocturnal vocalisation activity charts – important in interpreting the level of representation provided by each standard error bar.

Table 5.5: Summary of the presence and frequency of occurrence of each species at each study site.

	Tapir	Millionario	Cockspur Pond	Guava Pond	Warree Pond	Puzzle Pond	Marshy Pond	Aguada	Subway MPR
<i>Total number of repeats</i>	3	3	2	3	3	3	3	3	2
<i>Agalychnis callidryas</i>	0	0	2	3	3	3	3	3	0
<i>Agalychnis moreletii</i>	0	0	0	0	3	3	0	3	0
<i>Hyla loquax</i>	3	2	2	3	0	2	3	3	0
<i>Hyla microcephala</i>	0	1	2	3	0	0	3	0	2
<i>Hyla picta</i>	1	0	2	2	0	0	2	0	2
<i>Hyla ebraccata</i>	0	0	0	0	0	0	3	0	0
<i>Smilisca baudinii</i>	1	1	1	0	0	0	1	0	2
<i>Sinax staufferi</i>	0	0	0	0	0	0	0	0	1
<i>Gastrophryne elegans</i>	0	0	0	0	0	0	1	0	0
<i>Rana berlandieri</i>	1	2	2	2	0	1	0	2	2
<i>Bufo valliceps</i>	1	1	0	0	0	0	1	0	2
<i>Total number species</i>	5	5	6	5	2	4	8	4	6

1. Tapir Pond (Grid reference: 858 528).

As can be seen from the photograph and site map (Appendix 2 (i)), Tapir Pond is a large, open pond. It is semi-permanent in nature, being full for the duration of our study period but often remaining relatively dry during the wet season of other years (N.Bol pers. comm.). As can be seen

from the table in Appendix 3 it is quite a shallow body of water, never reaching more than ½ meter in depth. The vegetation is low around the edges, with extensive reed beds on the forest side and low grass by the roadside. The closed canopy of the forest is set back some 15 m from the edge of the pond. Although a road runs alongside the north edge of the pond, it can be seen to provide little disturbance to the amphibian community as we only observed 3 Forestry Department vehicles on it during our entire stay.

Table 6 gives the summary abundance and activity statistics for all species observed at Tapir Pond. Although it has one of the highest numbers of species of all the study sites, they were all found at relatively low abundances, and with a low level of vocalisation activity. Apart from *H.loquax* and *R.berlandieri* the other species called for less than 1/5th of the total recorded time at Tapir Pond (24 hours), suggesting a rather sporadic and inconsistent appearance. No one species attained an average maximum Vocalisation Category of greater than 1, emphasising a ubiquitously low amphibian abundance. The existence of persistent periods of complete inactivity at Tapir Pond is indicated by the very low mean Vocalisation Categories, taken from across all hours of each survey night. As noted above the essential use of data such as in Table 5.6, is in providing a capacity for assessing interannual variation in abundance and calling activity of local breeding aggregations. In so far as such measures are not absolute, and that the breeding aggregation at Tapir Pond does not necessarily represent a biologically distinct population, the values are more potentially useful, than of any immediate ecological interest when considering the status of local amphibian populations. Providing the same methodology is strictly adhered to, and observer error contributions remain consistent, it is perfectly acceptable to discuss population changes in relative terms – relative to our specific choice of sites, monitoring intensity, and sampling protocol. Although it has not been presented here, a useful comparison for future years would be to rank each species by ponds with respect to each index, and compare the series order across years, and the difference in its variance for each species. Figure 5.14 shows the temporal pattern of nocturnal vocalisation activity for all the species observed at Tapir Pond. The inconsistent appearance of each species across both different nights and different hours, means that most species are described using data from only one study night, and as such offer what is perhaps a weakly representative picture. However, it can be seen from comparing Figure 5.14 with Figures 5.7 & 5.8 that *H.loquax* and *H.picta* follow similar patterns to those observed at the larger spatial scale of the entire Las Cuevas site.

Table 5.6: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Tapir Pond.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Bufo valliceps</i>	2	5 (21)	0.667 (0.333)	0.208 (0.15)	0.583 (0.41)	0.583 (0.41)
<i>Hyla loquax</i>	3	15 (63)	1 (0)	0.625 (0.125)	2.333 (0.712)	2.333 (0.71)
<i>Hyla picta</i>	1	3 (13)	1 (0.577)	0.05 (0.25)	1.958 (1.238)	2.5 (1.282)
<i>Smilisca baudinii</i>	1	4 (17)	0.333 (0.333)	0.167 (0.167)	0.25 (0.25)	0.25 (0.25)
<i>Rana berlandieri</i>	2	12 (50)	0.667 (0.333)	0.5 (0.25)	1.25 (0.661)	1.25 (0.661)

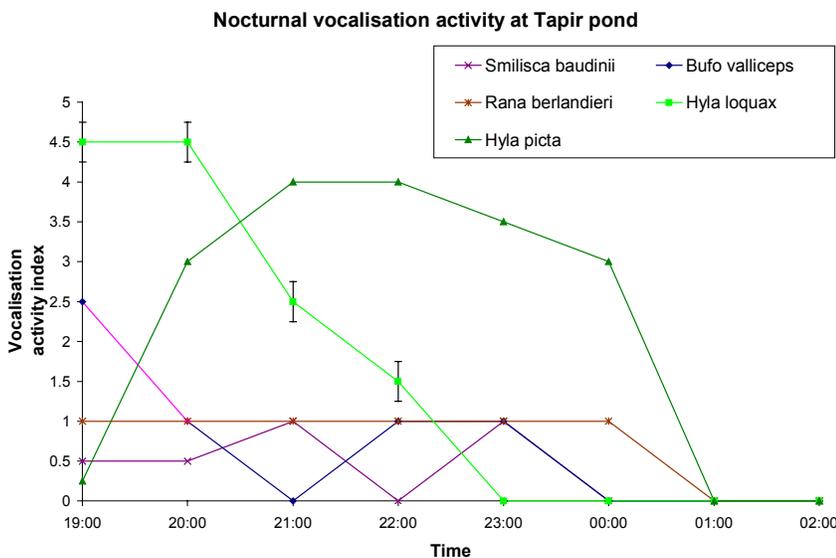


Figure 5.14: Nocturnal vocalisation activity (index) at Tapir Pond. Hourly values are taken across observations for each species during repeat study nights (including SE bars when possible).

2. Millionario (Grid Reference: 859 932)

Millionario is very similar in its physical characteristics to Tapir Pond – see Appendix 2 (ii). It is a large open body of water, close to the roadside and set about 15-20 m away from the forest edge. It differs from Tapir Pond in being both noticeably bigger and deeper, indicating its historical origin as a Mayan aguada - a fact that also helps explain its permanent nature. The edges of Millionario exhibit a similar vegetation type to Tapir Pond, with many reeds, and mixed grasses, but also dense bushes of Cockspur (*Acacia cookii*) and Hogplum (*Spondias mombin*) around the edges, providing much in the way of suitable cover and calling sites for amphibians.

Table 5.7 gives the summary abundance and activity statistics for all species observed at Millionario. Of the 5 species observed to be present *H.microcephala* and *R.berlandieri* are the most active with respect to the total number of hours heard calling. With respect to the average maximum Vocalisation Category *H.loquax*, *H.microcephala* and *R.berlandieri* are found persistently in the highest numbers, whilst the more erratic or explosive breeders, *B.valliceps* and *S.baudinii* (see above), are found both at low numbers and at low levels of vocalisation activity. This suggests that for the latter two species, either the local environment at Millionario is unsuitable and that their appearance represents chance events, or that they require particular climatic stimuli to become active, which were rarely experienced during the three repeats. The low number of hours in which *H.loquax* was heard, coupled with it having the highest values of mean calling intensity and activity, indicate that although it was a rather infrequent caller, when it did call it was invariably from within a relatively synchronous chorus of at least 6 individuals (VC = 2), and at a high level of intensity (thus making the average vocalisation index relatively high despite long periods of inactivity during later hours in the night).

Table 5.7: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Millionario.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Bufo valliceps</i>	1	7 (29)	0.667 (0.667)	0.417 (0.417)	1 (1)	1.583 (1.583)
<i>Hyla loquax</i>	3	21 (21)	1.333 (0.333)	1.042 (0.253)	4.292 (0.969)	5.46 (1.926)
<i>Hyla microcephala</i>	2	10 (42)	1 (0.577)	0.5 (0.289)	1.625 (0.82)	2.125 (1.192)
<i>Smilisca baudinii</i>	2	2 (8)	0.667 (0.333)	0.083 (0.042)	0.125 (0.82)	0.125 (1.192)
<i>Rana berlandieri</i>	3	11 (46)	1 (0)	0.458 (0.273)	1.5 (1.25)	1.5 (1.25)

Figure 5.14 shows the temporal pattern of nocturnal vocalisation activity at Millionario. *R.berlandieri* shows its typically late peak in calling (cf:Figure 5.12), and *H.microcephala* and *H.loquax* both exhibit early peaks (cf: Figures 5.7 & 5.9), although there is a considerable degree of variability across the different study repeats. One clear message that comes from this preliminary study, is that in order to maximise our insight into local site variability in activity patterns between years, the maximum number site repeats possible should be conducted to distinguish real underlying patterns from the influence of chance events.

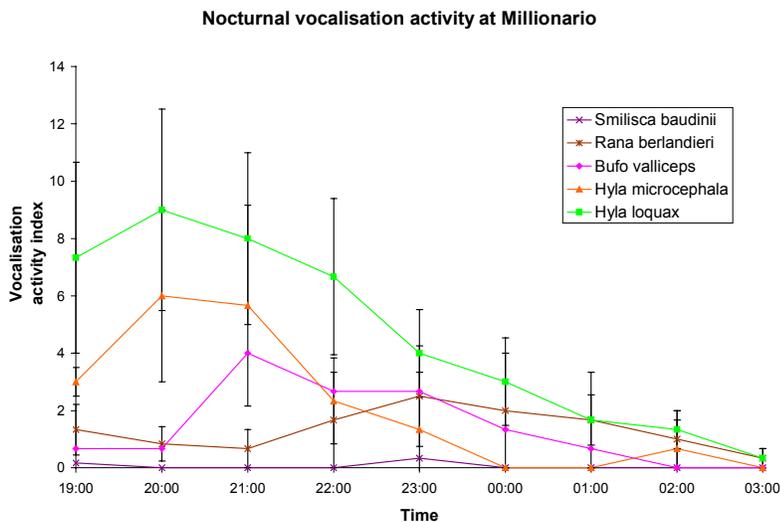


Figure 5.15: Nocturnal vocalisation activity (index) at Millionario. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available)

3. Cockspur Pond (Grid Reference: 859 533)

Cockspur Pond is one of the smallest study sites as can be seen from Appendix 2 (iii), and as its name suggests it is surrounded on all sides by a relatively dense thicket of Cockspur trees (*Acacia cookii*). However, despite its small size it was observed to be of semi-permanent status due a relatively large depth (see Appendix 3 (iii)). Like Millionario and Tapir Pond, it is situated in an open clearing next to the main San Ignacio road, roughly 30 m from the forest edge. Some 30-50% of the pond surface is taken over by a thick reed bed.

Table 5.8 gives the summary statistics of the frog species observed at Cockspur Pond, over the two repeats that were conducted. *H.microcephala* is clearly the most dominant species, with respect total number of hours recorded, relative abundance and overall vocalisation activity. The low mean vocalisation indices of many species indicates that most of their species records were from single individuals or small groups, each exhibiting low levels of infrequent calling activity. Apart from perhaps *R.berlandieri*, which for its size was seen in relatively high numbers and exhibited the second

highest calling rate, it is likely that due to its small size Cockspur Pond does not act as a focal breeding site for many individuals. Furthermore, infrequent and often lone visitors such as *S.baudinii* and *A.callidryas* were perhaps strays from other nearby bigger ponds (e.g. Millionaire or Guave Pond), or the result of periods of high activity during or after an intense rainfall. As can be seen from Appendix 1, Cockspur Pond is very close (< 50 m) from Guave Pond, so the opportunity for recording individuals which were active at both sites was high. This and the above points led to the abandonment of monitoring at Cockspur Pond after the second repeat in favour of Guave Pond.

Table 5.8: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Cockspur Pond.

Species	Number of nights observed (out of 2)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Agalychnis callidryas</i>	2	6 (38)	1 (0)	0.375 (0.125)	0.438 (0.188)	0.438 (0.188)
<i>Hyla loquax</i>	2	9 (56)	1.5 (0.5)	0.625 (0)	1.438 (0.188)	1.938 (0.312)
<i>Hyla microcephala</i>	2	12 (75)	1.5 (0.5)	1 (0.5)	2.675 (1.675)	4.125 (3.125)
<i>Hyla picta</i>	2	7 (44)	1.5 (0.5)	0.5 (0.375)	1.5 (1.375)	1.938 (1.813)
<i>Smilisca baudinii</i>	1	4 (25)	0.5 (0.5)	0.25 (0.25)	0.438 (0.438)	0.25 (0.25)
<i>Rana berlandieri</i>	1	8 (50)	1.5 (0.5)	0.625 (0.5)	1.875 (1.75)	0.625 (0.5)

Figure 5.16 shows the temporal pattern of vocalisation activity at Cockspur Pond taken from over the two repeats. In light of the small sample size of hourly recordings for each species, their low numbers, and infrequent visits, there is a consequent absence of a clear pattern for many species. However *H.microcephala* and *Hyla loquax* continue to reflect a similar pattern of early vocalisation activity as shown in the species accounts from across all pond sites, and *R.berlandieri* shows its characteristically late peak in activity (see Species Accounts).

Nocturnal vocalisation activity at Cockspur Pond

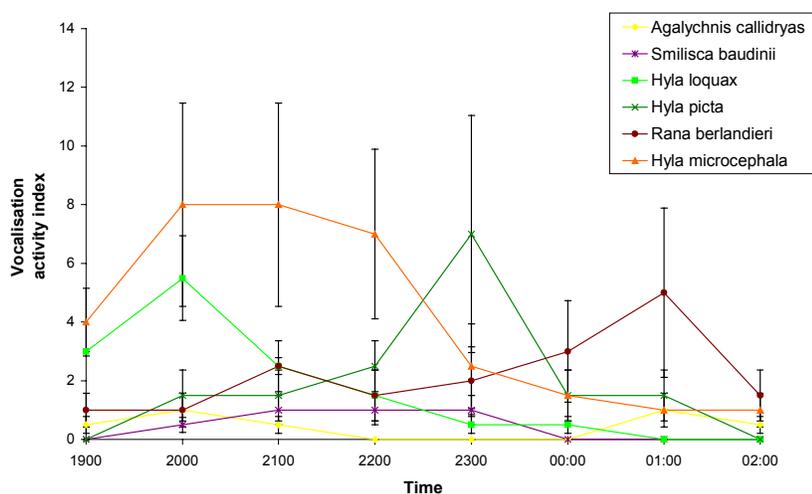


Figure 5.16: Nocturnal vocalisation activity (index) at Cockspur Pond. Hourly values are taken across observations for each species during repeat study nights. (including SE bars when available).

4. Guave Pond (Grid Reference: 859 533)

Guave Pond is almost unique amongst the 8 Las Cuevas study sites in that it is almost completely overgrown by dense low vegetation – dominated as the name indicates by Guave trees (*Psidium guajava*). It is of medium size, but considerably smaller than Millionario and Tapir Pond (see Appendix 2 (iv)), and is furthermore the only pond site to be situated next to a semi-permanent stream¹. Although no historical records exist the pond was classed as semi-permanent in that it contained at least 20 cm of water for the duration of our study period.

Table 5.9 gives the summary statistics of the frog species found to occur at Guave Pond over the 3 repeats. Although it was found to be less diverse than its immediate neighbour, Cockspur Pond, it hosted a much greater abundance of frogs and at considerably higher levels of vocalisation activity. Apart from the isolated appearances of *R.berlandieri* (possibly a ‘stray’ from Millionario), all other species called for at least half the total number of recorded hours. The high average maximum Vocalisation Category and high mean vocalisation indices shown for the first 4 species indicates a high level of temporal persistence in both the peak number of active males, and peak rate of vocalisation activity. Although with only few survey repeats and a relatively rough assessment of environmental and climatic variables it is difficult to elucidate the explanation for this high level of vocalisation activity, it is likely that the predominance of low lying dense vegetation provides both ideal calling and oviposition sites for many species (Lee 1996; Campbell 1998). Figure 5.17 shows the temporal pattern of nocturnal vocalisation activity at Guave Pond, across the 3 survey repeats.

¹ Owing to the limestone bedrock streams are rare in the Chiquibul Forest, with most flowing surface water quickly finding its way underground.

Despite high levels of between night variation in hourly activity levels, *H.loquax* and *A.callidryas* can be seen to peak characteristically early with *H.microcephala* and *H.picta* peaking shortly after.

Table 5.9: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Guave Pond.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Agalychnis callidryas</i>	3	19 (79)	1.333 (0.333)	0.875 (0.144)	2.583 (0.356)	3 (0.688)
<i>Hyla loquax</i>	3	23 (96)	1.667 (0.333)	1.167 (0.15)	4.143 (0.16)	5.477 (0.636)
<i>Hyla microcephala</i>	2	14 (58)	2 (0.577)	1 (0.375)	2.542 (1.027)	4.542 (2.09)
<i>Hyla picta</i>	2	10 (42)	1 (0.577)	0.75 (0.204)	2.375 (1.536)	2.375 (1.536)
<i>Rana berlandieri</i>	2	2 (8)	0.667 (0.333)	0.167 (0.11)	0.208 (0.11)	0.208 (0.11)

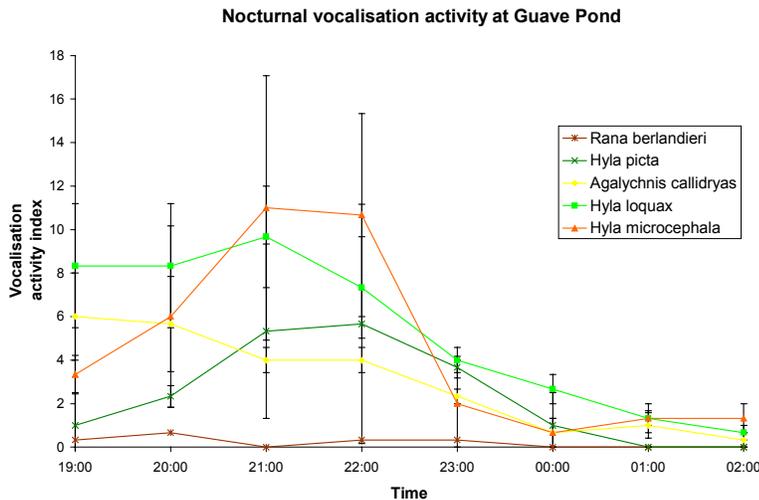


Figure 5.17: Nocturnal vocalisation activity (index) at Guave Pond. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available).

5. Warree Pond (Grid Reference: 883 515)

Whereas all the above pond accounts describe sites that are distanced from the main forest canopy, being situated on the roadside, Warree Pond is situated deep into the forest, with consequently at least 70% canopy cover. The limited availability of light precludes the presence of a dense understory, and the site is particularly notable from its lack of grasses, reeds, or shrubs. However, a number of low hanging palms surround the pond – both Give and Take Palm (*Cryosophila stauracantha*) and Bayleaf (*Sabal mauritiformis*), which are common plants of the local sub-canopy environment (see Appendix 2 (v)). The pond was classed as semi-permanent, although it is known

to dry up relatively quickly during the occasional mini dry season that can occur in mid-August (N.Bol pers. comm.).

Table 5.10 shows the summary statistics for the species found at Warree Pond over the 3 study repeats. Although only the two *Agalychnis* species were observed at this site, both were prominent during each of the surveys and throughout the majority of the evening, with *A.moreletii* in particular being heard for over 90% of the total recorded time. It is relevant to note here that the vocalisation of *A.moreletii* is very similar to that of *A.callidryas* and that the lack of existence of any recordings of *A.moreletii* prior to our arrival could have resulted in early misidentification of *A.moreletii* for *A.callidryas*, although practice was quickly acquired. However, despite the observed persistence in calling neither species was heard in high numbers, and for *A.callidryas* there was never more than 5 individuals. Furthermore the vocalisation activity was relatively low for both species. One possible explanation for this was that Warree Pond was noted to be highly active at the beginning of the wet season, but became quickly subdued with respect to both numbers of active individuals and calling rate. This re-emphasises that is important to complete a high number of repeat surveys of each study site during a monitoring program, not only to incorporate variation in climatic conditions but also to incorporate *seasonal* variation that may exist in the reproductive behaviour of these species. With respect to small, arboreal species such as those found at Warree Pond, vocalisation surveys may be the only feasible way to assess the status of populations, and as such it is crucial to understand temporal patterns in reproductive behaviour – not only in an attempt to assess the maximum number of individuals at a site, but also to ensure that surveys in future years are conducted at the appropriate time in the season to allow a fair comparison.

Table 5.10: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Warree Pond.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Agalychnis callidryas</i>	3	17 (71)	1 (0)	0.708 (0.182)	1.417 (0.083)	1.417 (0.083)
<i>Agalychnis moreletii</i>	3	23 (96)	1.667 (0.333)	1.333 (0.232)	2.708 (0.583)	4.167 (1.462)

Figure 5.18 shows the temporal pattern of nocturnal vocalisation activity of both species across the 3 survey nights at Warree Pond. Both species show a characteristically early peak accompanying gradual decline in vocalisation activity. This gradual decline in activity following the peak time appears to be highly characteristic of both *Agalychnis* species, and is in marked contrast to the relatively rapid drop off in activity by species such as *H.picta* and *H.microcephala*.

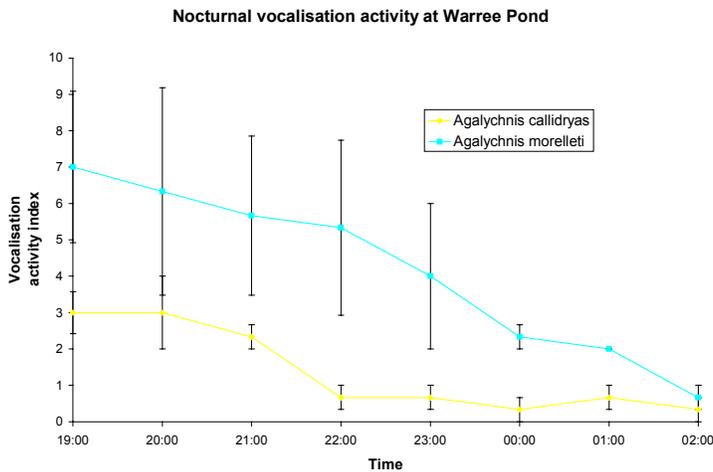


Figure 5.18: Nocturnal vocalisation activity (index) at Warree Pond. Hourly values are taken across observations for each species during repeat study nights.

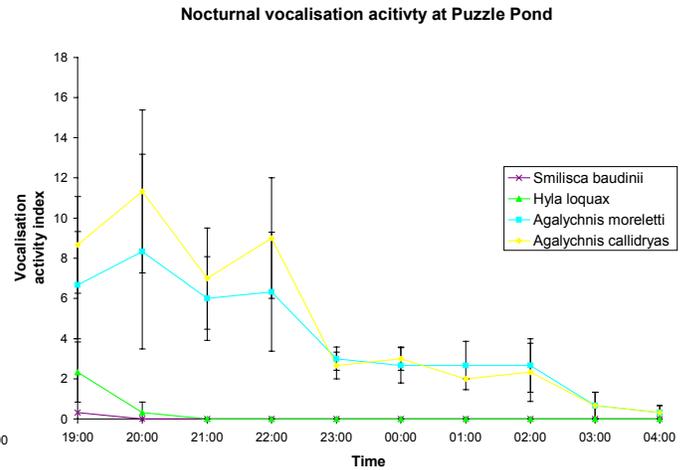


Figure 5.19: Nocturnal vocalisation activity (index) at Puzzle Pond. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available).

6. Puzzle Pond (Grid Reference: 908 515)

The surrounding environment to Puzzle Pond is almost identical to that of Warree Pond, with a relatively dense upper canopy cover, little shrub or herb-layer vegetation, and a noticeable dominance of palms (Appendix 2 (vi)). As can be seen from Appendix 3 (vi) the Pond was characteristically shallow, and its temporary nature was emphasised by the fact that it only appeared following an intense storm at the end of July.

The similarity between Puzzle Pond and Warree Pond shown by the vegetation is also reflected in the amphibian community, with Puzzle Pond also being dominated by the 2 *Agalychnis* species (Table 5.11). *H.loquax* made a few very infrequent appearances, suggesting that they were ‘stray’ recordings from the relatively abundant *H.loquax* congregations often found on the nearby Las Cuevas –

Monkey Tail road during rain events. In contrast to Warree Pond, both *A.callidryas* and *A.moreletii* were found at very similar levels of relative abundance, calling persistence, and mean vocalisation indices. This indicates that not only were the numbers of the two species roughly equivalent, but also that their vocalisation activity patterns were remarkably congruent, both in their shape and extent. This point is clearly demonstrated by Figure 5.19, which shows the mean hourly activity levels of both species to follow almost exactly the same temporal pattern. Such close concordance suggests the role of a common factor in shaping the vocalisation pattern of these two species. Such a factor could be abiotic relating to the weather conditions, or perhaps biotic, relating to the presence of a common predator. One of the intended improvements to the Project Anuran protocol during the second field phase is to collect more exact data on abiotic and biotic environmental variables, relating not only to this habitat but for all study sites.

Table 5.11: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Puzzle Pond

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Agalychnis callidryas</i>	3	23 (96)	2 (0.578)	1.333 (0.167)	3.708 (0.397)	5.75 (1.231)
<i>Agalychnis moreletii</i>	3	23 (96)	1.667 (0.667)	1.667 (0.167)	3.583 (0.56)	4.792 (1.458)
<i>Hyla loquax</i>	2	3 (13)	0.667 (0.333)	0.188 (0.05)	0.333 (0.05)	0.333 (0.22)

7. Marshy Pond (Grid Reference: 898 508)

Marshy Pond exhibits characteristics particular to a number of the other Las Cuevas Study sites. It is similar to Warree and Puzzle Ponds in that it is situated quite deep into the forest, although the canopy cover is significantly less as it is situated either side of the main forest track between Las Cuevas and the Monkey Tail River (see Appendix 2 (vii)). The opening of the canopy provides sufficient light for there to be a relatively dense shrub layer, not dissimilar to that at Guave Pond, and most characteristically as suggested by the name is a predominance of reed beds and marshy ground. As can be seen from the Appendix map (2: vii), the site is made up of a number of separate areas of shallow, standing water which indicate its highly temporary nature.

Marshy Pond exhibits the highest frog diversity of all the Las Cuevas study sites, a consequence perhaps of the unique combination of closed canopy and open site vegetation and physical features. Furthermore its geographic location, and position on the main path suggest that it may be accessible to a larger frog species pool than the other study sites. Table 5.12 shows the summary statistics for the species found at Marshy Pond over the 3 repeats. A number of species present are in notably low numbers, largely due to their sporadic or explosive breeding patterns (see Species Accounts). Predictably these species are *B.valliceps*, *S.baudinii* and *G.elegans*, all of which have low mean vocalisation indices, and are heard for a relatively short period of time. *A.callidryas* has an equally low set of vocalisation indices, but a high persistence of calling activity, being heard for some 88% of the total number of hours recorded. These facts indicate that few *A.callidryas* individuals were present but those that were could be commonly heard throughout the night— as seen above in both Warree and Puzzle Ponds. Table 5.12 clearly shows that the site was dominated by 3 relatively abundant and highly active species—*H.ebraccata*, *H.microcephala*, and *H.picta*. The former two were clearly the most common and active species at Marshy Pond, having both the highest average maximum Vocalisation Category across the 3 study nights, and by far the highest rates of vocalisation activity. As noted in the Species Accounts, it is pertinent to re-emphasise that the acoustic properties of *H.ebraccata* and *H.microcephala* are very similar, and as a consequence both species are recognised to compete strongly both between and within each species to avoid acoustic interference (Wells & Schwartz 1984; Schwartz & Wells 1985). This interaction can lead to high levels of aggressive calling both between and within either species, especially when heard in chorus (Schwartz & Wells 1985), pointing towards caveats in interpreting the vocalisation intensity or activity indices. It is interesting to note also that Marshy Pond was the only place in the entire vicinity of Las Cuevas where *H.ebraccata* was found, although why this would be is not obvious. It is possible that its appearance is due to the rather unique characteristics of Marshy Pond noted above, or perhaps more simply due to a limit in the number of study sites we observed. Figure 5.20 shows the temporal pattern of vocalising activity at Marshy Pond. As expected in light of the above comments, the pattern of activity for *H.ebraccata* and *H.mirocephala* is highly congruent, with *H.picta* showing a notably later peak as indicated by its observed behaviour across all sites (cf: Figure 5.8).

8. Aguada (Grid Reference: 912 517)

As the name suggests the Aguada is an old Mayan reservoir, and is located just off the main track between Las Cuevas and Monkey Tail River, about 1.5 miles from the river itself. The surrounding vegetation is very similar to that found at Warree Pond and Puzzle Pond, with little understory

vegetation, and a considerable number of palms, including a large Cahune Palm (*Attalea cohune*). The site was classes as semi-permanent rather than permanent, as although once filled it persisted for a long time, it required a succession of heavy storms to start collecting water.

Table 5.12: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Marshy Pond

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Bufo valliceps</i>	1	4 (17)	0.333 (0.333)	0.167 (0.167)	0.292 (0.292)	0.292 (0.292)
<i>Agalychnis callidryas</i>	3	21 (88)	0.333 (0.333)	0.125 (0.125)	0.292 (0.292)	0.292 (0.292)
<i>Gastrophryne elegans</i>	1	3 (13)	1.333 (0.333)	0.958 (0.042)	2.292 (0.273)	2.708 (0.579)
<i>Hyla ebraccata</i>	3	21 (88)	2 (0.578)	1.292 (0.341)	3.541 (0.708)	6.042 (1.991)
<i>Hyla loquax</i>	3	12 (50)	1 (0)	0.5 (0.191)	1.5 (0.505)	1.5 (0.505)
<i>Hyla microcephala</i>	3	21 (88)	2.667 (0.333)	1.5 (0.144)	4.167 (0.6)	7.912 (0.694)
<i>Hyla picta</i>	2	12 (50)	1 (0.578)	0.708 (0.48)	2.765 (2.029)	3.135 (2.996)
<i>Smilisca baudinii</i>	2	12 (50)	0.667 (0.333)	0.5 (0.26)	1.042 (0.579)	1.0417 (0.579)

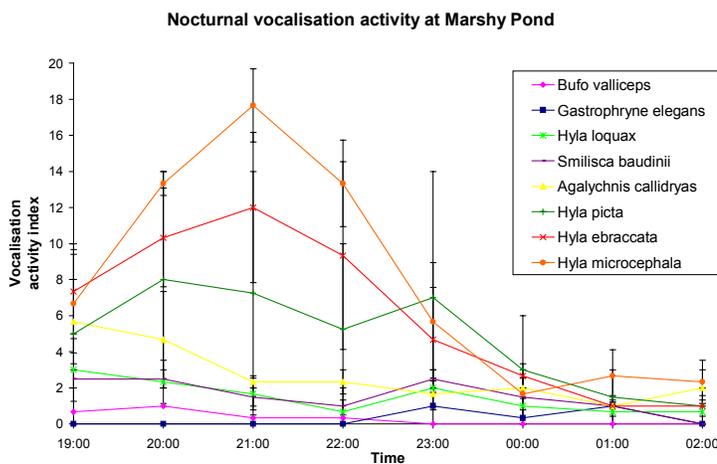


Figure 5.20: Nocturnal vocalisation activity (index) at Marshy Pond. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available).

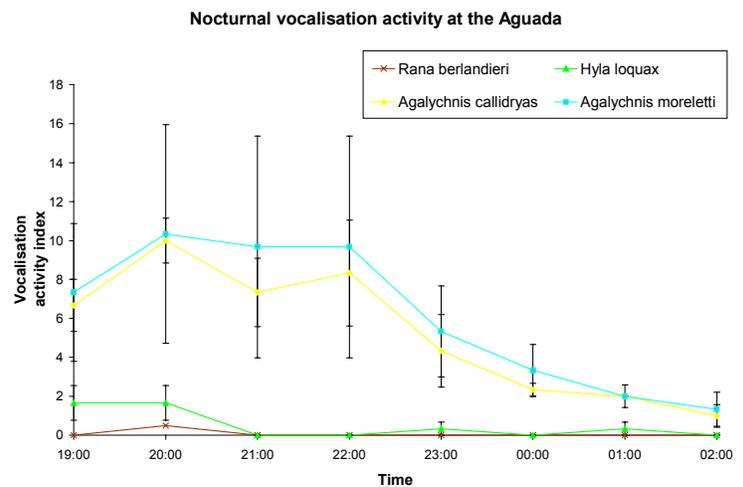


Figure 5.21: Nocturnal vocalisation activity (index) at the Aguada. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available).

In keeping with the observed similarities with Warree Pond and Puzzle Pond, the Aguada is dominated by *A.callidryas* and *A.moreletii*, with the occasional appearance of the ubiquitous *H.loquax* (Table 5.13). However, both *Agalychnis* species are present in significantly greater numbers at the Aguada than at any other site around Las Cuevas, and consequently the observed levels of vocalisation activity are notably high. One rather obvious potential reason for this discrepancy is that the Aguada is significantly bigger than either Warree Pond or Puzzle Pond. Figure 5.21 shows the temporal pattern of vocalisation activity at the Aguada, taken from across the 3 study repeats. It is interesting to note that the same high degree of congruence between *A.callidryas* and *A.moreletii* noted at Puzzle Pond is evident at the Aguada. In light of the fact that both sites have exactly the same species composition (essentially just these two), the similarity is perhaps more due to biotic interactions, or more explicitly, the *absence* of biotic interactions in relation to other sites which have more species, all of which are potentially competing for acoustic calling ‘space’.

Table 5.13: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at the Aguada.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Agalychnis callidryas</i>	3	23 (96)	2 (0)	1.333 (0.11)	3.292 (0.253)	5.292 (0.723)
<i>Agalychnis moreletii</i>	3	23 (96)	2 (0.577)	1.417 (0.37)	3.458 (0.897)	6.125 (3.138)
<i>Hyla loquax</i>	3	6 (25)	1 (0)	0.25 (0.072)	0.458 (0.22)	0.458 (0.22)

9. Subway MPR (Douglas Da Silva Forest Station) (Plate 5; F)

Subway MPR is additional site which was spontaneously surveyed during an enforced stay at the Forestry Department station whilst Las Cuevas was temporarily closed. In light of its unique environment and geographic location with respect to the Las Cuevas sites, we hope to make it a permanent addition to the Project Anuran monitoring program, and therefore have reported the summary statistics and activity chart for its species assemblage. As can be seen from the photograph in Plate 5, Subway MPR is a far cry from the habitat around Las Cuevas, being both highly

disturbed² and surrounded on 3 sides by *Pinus carribea* savanna, rather than broadleaf deciduous forest. The site comprises a very temporary patch of standing water, throughout which grasses and reeds can be found as the ground remains wet and marshy for most of the year. Aside from the *Pinus carribea* habitat the site is about 200 m from an significant stretch of broad-leaved gallery forest which borders the Rio Frio River.

Table 5.14 shows the summary statistics for the species found at Subway MPR, taken from across the 2 survey repeats. The site exhibited a complement of species that was unique to any found in the vicinity of Las Cuevas, including the previously unrecorded *Scinax staufferi*. The relative abundance and vocalisation activity recordings are biased in that both survey nights were conducted in short succession, and immediately following a period of heavy rainfall. The site was dominated by *S.staufferi*, *H.microcephala*, and *R.berlandieri*, with the more occasional appearance of *H.picta* and *S.baudinii*. Although the temporal patterns of vocalisation activity observed in Figure 5.22 are similar to what is expected for most species (e.g. late calling peak in *R.berlandieri*), it is interesting to note that the vocalisation activity of *S.staufferi* is seen to be the most persistent and highly active example of all the species presented in this report.

Table 5.14: Summary relative abundance and vocalisation activity data for all species observed during three repeat surveys at Subway MPR.

Species	Number of nights observed (out of 3)	Total number hours called (% of maximum)	Maximum Vocalisation Category averaged across all nights in which the species was observed (+/- SE)	Mean Vocalisation Category attained in any one night when present (+/- SE)	Mean Vocalisation Intensity attained in any one night when present (+/- SE)	Mean Vocalisation Activity (index) attained in any one night when present (+/- SE)
<i>Bufo valliceps</i>	1	2 (13)	0.5 (0.5)	0.125 (0.125)	0.375 (0.375)	0.375 (0.375)

² To readers familiar with the city of Edinburgh the name ‘Subway’ comes from a nightclub following the incessantly loud music that was played at the site by the forest rangers.

<i>Hyla microcephala</i>	2	15 (94)	2.5 (0.5)	1.438 (0.063)	4.188 (0.688)	6.688 (0.313)
<i>Hyla picta</i>	2	7 (44)	1 (0)	0.438 (0.313)	1.063 (0.938)	1.063 (0.938)
<i>Scinax staufferi</i>	2	16 (100)	3 (0)	2.25 (0.125)	5.563 (0.813)	12.25 (1.125)
<i>Smilisca baudinii</i>	2	11 (69)	1 (0)	0.688 (0.188)	1.688 (0.563)	1.688 (0.563)
<i>Rana berlandieri</i>	2	12 (75)	1.5 (0.5)	0.973 (0.403)	3 (1.875)	4.188 (3.063)

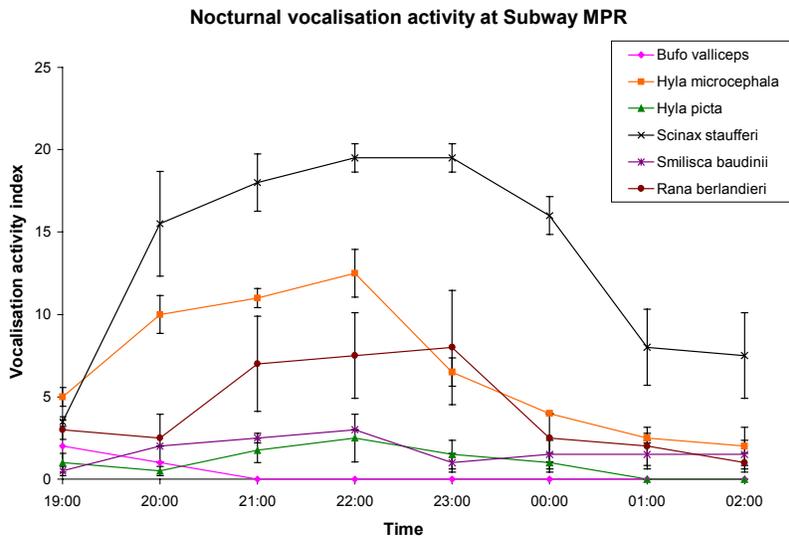


Figure 5.22: Nocturnal vocalisation activity (index) at Subway MPR. Hourly values are taken across observations for each species during repeat study nights (including SE bars when available).

Analysis of Community Structure

It has already been repeatedly emphasised that an appreciation of the contribution of local processes in structuring the composition and population dynamics of local species assemblages, is a crucial step in understanding, predicting and even ultimately preventing amphibian population declines. An understanding as to the importance of local abiotic environmental features in determining temporal and spatial dynamics is needed in order to assess the relative impact of changes in global environmental features, such as UV-B, rainfall pH, interannual climatic patterns etc. Furthermore, in order to assess the implications of one population decline on the community structure and composition of all other local amphibians, it is necessary to gain an appreciation of the strength of biotic interactions in both the spatial and temporal segregation of amphibian communities. As discussed in Chapter 1 amphibians often play crucial roles in the nutrient and energetic dynamics of ecosystems. Consequently, any significant alterations in the lifetime reproductive success of one species following the demise of another, could not only have drastic implications for the amphibian community, but also for the rest of the ecosystem as a whole.

For the purposes of this report consideration of the community structure of Las Cuevas amphibians is taken with respect to two directions; (1) interactions between different amphibian species, and (2) interactions between amphibian populations and their environment.

1) Inter-specific interactions between vocalising amphibian species local to Las Cuevas

With the advent of multivariate statistics and increasingly sensitive tests for associations between multiple independent and even dependent variables, there are a seemingly infinite number of comparisons one could make. However, for the purposes of this report, the above data has been analysed with respect to; a) the temporal partitioning of the community, and b) the spatial partitioning of the community.

a) Temporal partitioning of amphibian vocalisation activity

It is clear from the results and interpretation in the Species and Site accounts that a marked degree of temporal partitioning exists between species with respect to the timing of peak reproductive activity. Figures 5.23 and 5.24 summarise this data across all study nights in which each species was observed, and illustrate peaks in Vocalisation Category and Vocalisation Activity respectively in reference to the 24-hour clock.

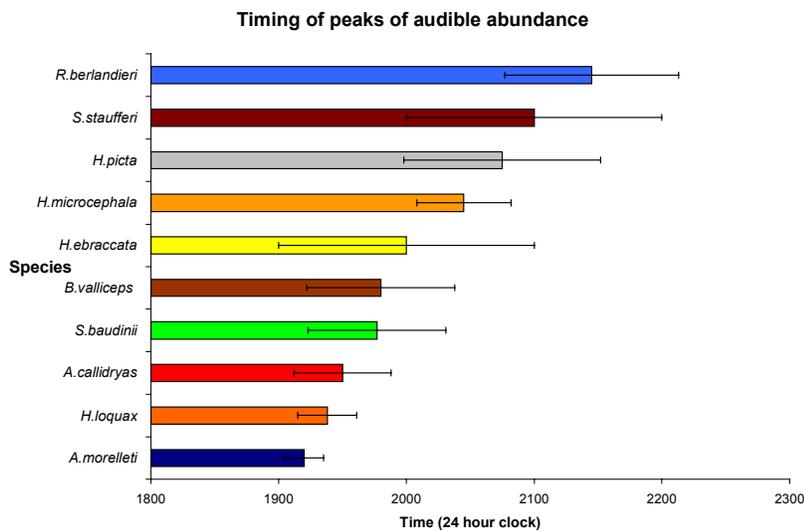


Figure 5.23: Timing of the peak in audible abundance (Vocalisation Category) for all species including standard error bars. Data is from across all survey nights in which each species was found (see Table 5.4)

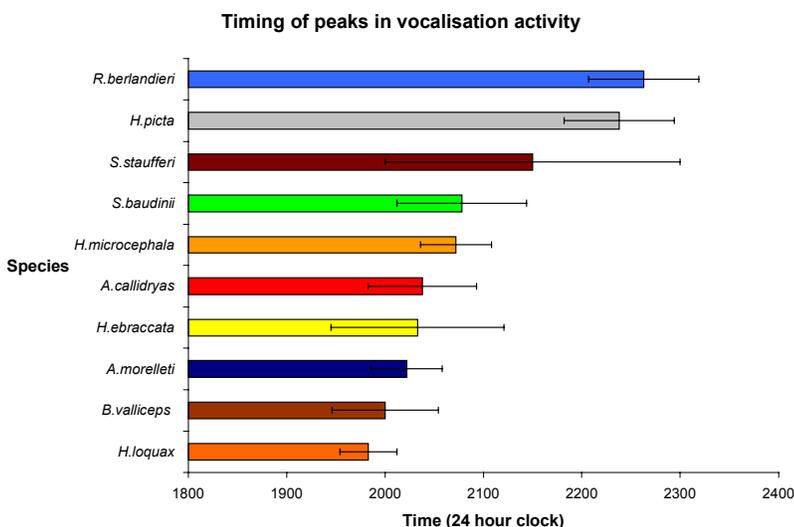


Figure 5.24: Timing of the peak in Vocalisation Activity for all species including standard error bars. Data is from across all survey nights in which each species was found (see Table 5.4)

As expected following the earlier results, there is a clear difference in the peak of both the relative number of active males, and the extent of their vocalisation activity. The two indices show relatively close congruence, again as expected, although it is understandable that the change in the frequency of vocalisation would occur at varying rates between species following the arrival of all males to a breeding site. The species which have been surveyed on the most number of occasions – *H.loquax*, *A.callidryas* and *H.microcephala*, all exhibit relatively small standard error bars for both charts – indicating that the high level of variance and apparent temporal overlap in the peaks of other species such as *H.ebraccata*, *Scinax staufferi*, and *H.picta* is at least partly due to their relatively small sample size (see Table 5.4). Interpretation of this result in the context of amphibian population dynamics and monitoring programs is made below in Chapter 6.

b) Spatial partitioning of the amphibian community.

It is useful to test whether separate species have their own specific habitat requirements, are distributed randomly, or whether particular groups of species covary in their spatial distribution due to either strong biotic interactions or common environmental requirements. An insight into this is vital for determining the consequences on amphibian community of changes in the local environment, or the loss of one particular species. Furthermore, it can afford some appreciation as to the role of local versus regional process in the spatial structuring of amphibian communities, and as such the implications for local population declines on the overall species status. Figure 5.25 shows a Multi Dimensional Scaling Plot, which is an ordination technique used to assess the degree of co-occurrence of different species across all sites. A clustering of points for certain species signifies that they are frequently found at the same site, thus suggesting the role of a common factor in determining their spatial distribution.

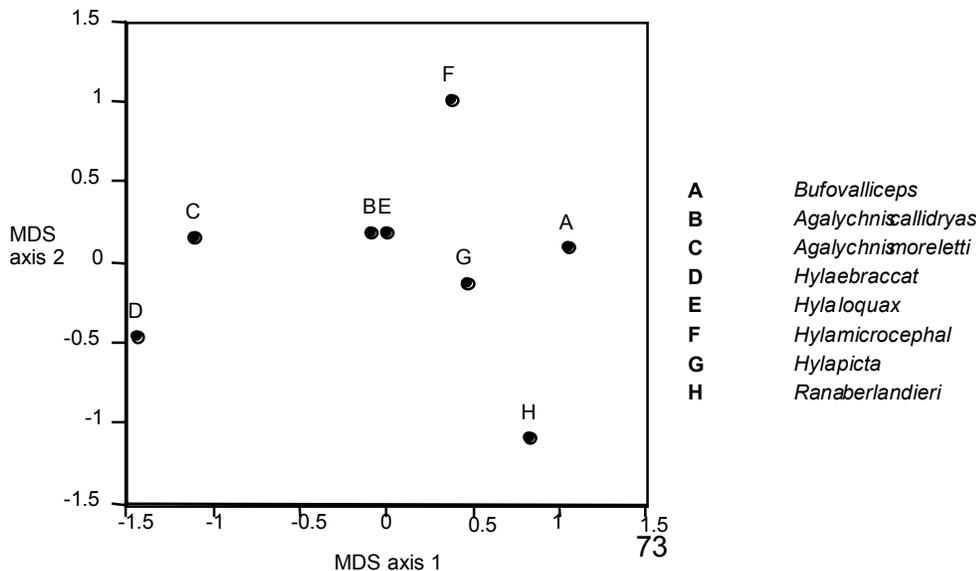


Figure 5.25: A Multi Dimensional Scaling plot (MDS) of the mean Vocalisation Categories of the 8 most prominent species across 9 study sites, using a Pearson's Correlation Matrix. Data is omitted from *S.staufferi*, *S.baudinii*, *G.elegans*, and *R.vaillantii*, as the poor representation of these species would be likely to bias the ordination of the other species.

It can be clearly seen from Figure 5.25 that there exists no distinct co-variance between the spatial arrangement of any particular groups or assemblages of species. See Chapter 6 for interpretation of this in the context of the Las Cuevas amphibians and their monitoring.

2) Interactions between amphibians and their environment

In order to assess the importance of local habitat conditions, and the consequent implications of their potential degradation, it is important to analyse relationships between both relative amphibian abundance and vocalisation activity, and biotic and abiotic environmental variables. Furthermore, it is equally of interest to assess the importance of temporally varying climatic conditions on the stimulation of reproductive activity. With respect to the abiotic environment, data was collected on an hourly basis with respect to water temperature, air temperature, and relative humidity, in conjunction with each record of frog abundance and vocalisation activity. Further data was collected during each survey night on the pH and conductivity of the pond, and pond depth, moonphase, and rainfall (volume and duration) (see Appendix 3 for all raw data). Due to equipment failure and error data for relative humidity, pH and conductivity was deemed to be useless and as such has been discarded. Action has been taken to ensure that improvements can be made on this front during Phase II. Due to limitations of time comparisons presented in this document are limited to that for rainfall. Future deliverables and reports from Project Anuran will incorporate an indepth assessment of amphibian communities with the other variables- greatly strengthened by more data due to be collected during Phase II.

The simplest and perhaps most intuitive way to compare patterns of amphibian abundance and vocalisation activity against rainfall is through Correlation analysis (Donnelly & Guyer 1994). The coefficients produced for both the mean Vocalisation Category and mean Vocalisation Activity index from across all recordings of each species during each survey night, against the rainfall volume, duration and intensity collected for the same days is given in Table 5.15. Comparisons are made against the rainfall duration (hours) and intensity (mm/hour) in addition to the volume per se, following anecdotal observations that the vocalisation activity of many amphibians seemed to respond to the *pattern* of rainfall above simply its amount. It is acknowledged that such comparisons

are greatly affected by the particular species composition and even particular individuals that were being surveyed during any one night. However, it is hoped that the relatively random order of ponds under survey, in addition to a relatively high number of repeats, is enough to identify any underlying pattern that may exist. A suggestion for improvement that came from this is to monitor one site under a higher frequency than the rest, in order to make future environmental comparisons that are free from confounding differences in species composition.

It can be seen from Table 5.15 that a significant degree of variation exists in the response of different species to changes in rainfall volume or pattern. This is unsurprising due to the myriad of other confounding factors which influence the reproductive activity of amphibians, in addition to the small sample sizes and sampling error in both amphibian populations and rainfall data. See Chapter 6 for interpretation of these results.

Table 5.15: Correlation coefficients from correlations between the relative abundance and vocalisation activity of each species and rainfall attributes.

Species	Correlation of Mean Vocalisation Category with:			Correlation of Mean Vocalisation Activity (index) with:		
	Volume rainfall (mm)	Hours rainfall	Intensity rainfall (mm/hour)	Volume rainfall (mm)	Hours rainfall	Intensity rainfall (mm/hour)
<i>Bufo valliceps</i>	0.138	0.176	0.589	-0.253	-0.215	-0.215
<i>Agalychnis callidryas</i>	-0.101	-0.041	-0.153	-0.528	-0.487	-0.479
<i>Agalychnis Moreletii</i>	0.52	0.492	0.408	0.127	0.204	-0.129
<i>Hyla loquax</i>	0.368	0.579	0.214	0.329	0.598	0.137
<i>Hyla picta</i>	0.149	-0.007	0.319	0.058	-0.239	0.425
<i>Hyla microcephala</i>	-0.274	0.062	-0.513	-0.482	-0.176	-0.645
<i>Hyla ebraccata</i>	0.305	0.305	0.305	0.5	0.5	0.5
<i>Gastrophryne elegans</i>	-	-	-	-	-	-
<i>Scinax staufferi</i> ³	-	-	-	-	-	-

³ *Scinax staufferi* was only observed at Subway MPR and is included here for comparison.

<i>Smilisca baudinii</i>	-0.0449	0.486	-0.483	0.499	0.787	-0.146
<i>Rana berlandieri</i>	0.114	0.127	0.484	0.529	0.823	0.143

Field Study 2: Non-vocalising and leaf litter species

As shown in Table 5.1, 5 species of non vocalising anurans were found during the entire study period. The 5 species are isolated in Table 5.16:

- | |
|---|
| <ul style="list-style-type: none"> • <i>Eleutherodactylus chac</i> • <i>Eleutherodactylus laticeps</i> • <i>Eleutherodactylus sabrinus</i> • <i>Eleutherodactylus sandersoni</i> • <i>Rana juliani</i> |
|---|

Table 5.16: Non-vocalising anurans species found during the entire study period.

Assessment of non-vocalising and leaf-litter species was made primarily using a intensive searching technique of sample plots from the vicinity of Las Cuevas (see Chapter 4). However out of a total of 51 plots and at least 120 man hours of searching, only 7 *Eleutherodactylus* individuals were found, with a further 4 observations from anecdotal sightings. The species found were:

- *Eleutherodactylus chac*: 2 individuals
- *Eleutherodactylus laticeps*: 4 individuals (3 in plots)
- *Eleutherodactylus sabrinus*: 5 individuals (2 in plots)
- In addition to this, one group of 15 juvenile suspected *Eleutherodactylus sandersoni* were found on the banks of the Monkey Tail branch of the Macal river during a river trip.

Our finding of only these 11 individuals raises a number of points and questions. Firstly it would be clearly unfeasible to conduct any analysis on such small numbers, whether in an attempt to describe the relative abundance of these species or their habitat associations. In this respect, this part of the project could be considered failing in its ability to meet the primary aims; to give an insight to the relative abundance and micro-habitat requirements of the leaf litter species, and as such a lot of the data collected stands to waste. However, such an intensive assessment was vital in an area almost completely undescribed for this species group. Such low numbers can of course point to two conclusions. Firstly, that leaf litter frogs are simply very rare in the area around Las Cuevas. *Eleutherodactylus sabrinus* and was only ever found in the close vicinity of moving water, and there are only two rivers in the vicinity of the study sites and a notable lack of any streams; temporary or permanent. However *Eleutherodactylus laticeps* and *Eleutherodactylus chac* were both found at least 8km from known moving water. If these species are present in any abundance then one is led to the

second conclusion – that unsuitable methods were employed. Although the same methods have been employed with success in other neo-tropical forests (e.g. Toft 1980b; Rand & Myers 1991), as stated above this group of species is notoriously difficult to monitor and despite being the world's most diverse vertebrate genus (Lee 1996), species of the genus *Eleutherodactylus* are almost without exception, extremely cryptic. However, it seems unlikely under this initial consideration that large populations do exist owing to the extreme difference in results between our data and that obtained from analogous studies.

Drift net fences: In total 60 trap nights were recorded from four different trap arrays (one trap night = one trap array of 6 traps monitored for one night). Only one species was caught, and on only three nights. The species was *Gastrophryne elegans*, the Elegant narrow-mouth frog, with catches of 8, 3 and 1 individual respectively. This in itself is a significant result as the species is described as rare by all guide books – indeed prior to 1996 it was described as being sighted only once in Belize in 1959 (Meyer & Foster 1996) (although this probably largely attributable to a lack of study).

Artificial cover traps: Only one individual was found underneath artificial cover during 5 days of monitoring – a juvenile *Bufo marinus*, a species which although is highly abundant in other areas appeared to be relatively scarce in our study area.

In total 8 voucher specimens were collected under license;

- 1 x *Eleutherodactylus chac*
- 2 x *Eleutherodactylus laticeps*
- 2 x *Eleutherodactylus rugulosus*
- 2 x *Rana juliani*

These specimens have been deposited in the Natural History Museum as part of their official collection. The taking of these specimens was deemed justified in consideration of the taxonomic questions surrounding the *E.rugulosus* group, and as such the advantage these individuals can afford research groups in the future. The 2 Ranids were taken for different reasons. One of them is undisputedly *Rana juliani* an endemic from the pine forests of Belize (MPR) (Lee 1996; Lee 2000). However the other is intriguing; although appearing at first sight to be *R.juliani*, it is noticeably distinct by its very small tympanum. A similar individual has also been photographed on the Raspaculo river (P.Stafford pers. comm.). Analysis of the specimen by Professor Julian Lee at the University of Miami suggests that it is a juvenile *R.vaillanti* specimen, although this is far from certain – especially as *R.vaillanti* juveniles are not known to exhibit gross variance in the size of the tympanum (P.Stafford pers. comm.). As noted in Chapter 3, Project Anuran Phase II hopes to find

further evidence of this potentially new species through further searches of the area in which it has been found (both MPR and the banks of the Raspaculo River). There is also opportunity to conduct a DNA kinship analysis by Dr Aulay Mackenzie at the University of Essex, should enough tissue from sufficient specimens be collected.

Chapter 6: Discussion

In order to appreciate the wider relevance of the detailed results presented in Chapter 5, it is important to consider them with respect to the present understanding of amphibian ecology, and the importance of such an understanding in studying the declining amphibian phenomenon. A brief discussion is given here to summarise our findings in this context, with respect to the diversity, relative abundance, and community structure of amphibians around Las Cuevas.

The diversity, relative abundance and community structure of the amphibian community at Las Cuevas

The total of 20 species of anuran amphibians found in the vicinity of Las Cuevas serves to highlight it as one of the most diverse areas with respect to amphibian fauna throughout the whole of Belize (Miller & Miller 1995). Of these 20 species, comprehensive relative abundance and reproductive activity data was collected for 9 of the vocalising species, with the remaining 11 being recorded either very infrequently at breeding sites, during nocturnal plot searching, or from anecdotal observations. Detailed discussion of the relative abundance and distribution of each species is given in Chapter 5, and the reader is referred to the individual accounts. The observation of a number of species in relatively high numbers, which were previously thought to be rare throughout the Yucatan, further serves to highlight the regional importance of the Las Cuevas area with respect to amphibian diversity. Perhaps the most interesting discoveries were of seemingly abundant populations of *Agalychnis moreletii*, *Gastrophryne elegans*, and *Smilisca cyanosticta*, all of which have been reported rarely in Belize (Lee 2000). It is likely that the restricted geographic distribution and relatively specialised habitat requirements (see Chapter 5) of these species have resulted in a biased picture of their status. This point re-emphasises the importance of multi-site comprehensive monitoring programs such as this one in allowing an assessment of the entire amphibian community, rather than simply a biased picture of its more prevalent members.

Although data on the diversity, relative abundance and habitat distribution of amphibians is central to any monitoring program, its interpretation with respect to the population dynamics of each species requires the collation of a number of years of data. However, as noted in Chapter 1, one of the main challenges facing biologists concerned with the declining amphibian phenomenon is in the

detection of real population declines from natural or stochastic fluctuations. It is therefore essential to gain an understanding of the variability in both the temporal and spatial population dynamics of the populations that are under surveillance. Such an understanding can be gained from an appreciation of the importance of local environmental characteristics and biotic interactions in structuring amphibian communities. Understanding the relative importance of such factors in community ecology is necessary to allow prediction as to potential effect of global environmental changes, as well as the consequences of alterations in population size and reproductive activity on the dynamics of the rest of the community. In light of this, it is therefore of interest to interpret the results with respect to the ecological structure of the amphibian communities local to Las Cuevas, as a valuable output of this project above simply reporting summary population statistics for each species and site (see Chapter 5).

As noted earlier, interpretation of the population dynamics of the species in this study is restricted to observations taken at breeding ponds. Although the importance of other habitat components is of undeniable importance, it is thought that in capturing the dynamics of crucial recruitment processes, such a focus provides an insight into the primary influences which determine the overall population dynamics (Marsh & Trenham 2000). The majority of studies on amphibian communities have reported that both spatial and temporal differences in resource use are important in allowing the coexistence of syntopic species at breeding ponds (Blair 1961; Bowker & Bowker 1979; Donnelly & Guyer 1994). With relevance to the vocalisation activity results of this study, it is thought that the characteristics describing the breeding call are some of the most important reproductive isolating mechanisms that allow amphibian coexistence (Fouquette 1960). Consequently an understanding of the vocalisation activity patterns of different species is central to understanding the strength of inter-specific biotic interactions, and hence the implications for overall reproductive success and population stability following alterations to the local environment.

It is clear from the summary diagrams of Figures 5.23 and 5.24 that the species observed at Las Cuevas exhibit a marked temporal partitioning with respect to the timing of peak reproductive activity. This is a particularly remarkable result as the average peak values are taken from across all survey nights, thus encompassing not only a range of different habitat types, but also different climatic conditions, and different times in the throughout the breeding season. There are two possible ecological explanations for this phenomenon. Firstly, that different species are responding

to temporal differences in the abiotic environment, such as air or water temperature or atmospheric humidity. However, although a detailed comparison of such variables against vocalisation activity has not been made, both preliminary analyses and previous work suggest that this is highly unlikely (see Williams & Hero 2001 for a recent assessment of the role of environmental determinants in amphibian communities). The second explanation is that the temporal partitioning is a result of interspecific competition for uninterrupted calling space or 'windows' – an interpretation that has been made by a number of other studies (Bowker & Bowker 1979; Aichinger 1987; Rand & Myers 1990; Donnelly & Guyer 1994). If this explanation is correct, then the fact that there is a notable distinction in the timing of peak reproductive activity for most species (Figures 5.23 & 5.24), suggests that the majority of frogs at Las Cuevas have been subject to such a selection pressure from the majority of the other species. If local habitat characteristics played an important role in differentiating the spatial distribution of the different frog species, one would expect that non co-occurring species would not be under any selection pressure for the temporal segregation of calling peaks, and as such would not be expected to exhibit any differences in vocalisation activity. Further evidence for the apparently weak role of local environmental characteristics (physical pond attributes, floral composition etc) comes from the ordination of relative abundances in Figure 5.25, which shows no marked clustering of different species groups. It should be noted here that this figure needs to be interpreted with caution, as it is limited to data from only 8 sites and any existing underlying pattern may simply be confounded by the small sample size.

It is clear from the figures presented under the Species Accounts in Chapter 5, that the degree of congruence in temporal calling patterns is highly variable between different species. Species such as *A.callidryas*, *H.microcephala* and *H.loquax* all show relatively close concordance in their vocalisation activity, whereas species such as *S.baudinii* and *B.valliceps* show almost no agreement. A convincing explanation for this is that the former species are classic examples of prolonged breeders, whereas the later are classic examples of explosive breeders (*sensu* Wells 1977; but see also Donnelly & Guyer 1994). Prolonged breeders, which call persistently throughout a significant proportion of the breeding season, are likely to be under considerably more selection pressure to segregate their temporal calling activity than explosive breeders, which breed in mass congregations, relatively infrequently, and usually in response to a climatic stimulus such as heavy rainfall. In light of the strong response of reproductive activity in explosive breeders to temporally varying climatic factors, it seems again unlikely that local environmental characteristics would exert an overriding influence

on their spatial distribution. It is interesting to note that all the explosive breeders observed at Las Cuevas have either a very loud (e.g. *R.dorsalis*, *B.valliceps*, *S.bandinii*) or distinctive (*G.elegans*) vocalisation, a characteristic which is perhaps the result of selection for a call which has overriding acoustic properties - in order to help guarantee a measure of reproductive success when the chance (appropriate climatic conditions) is presented.

A number of factors exist which may confound attempts to identify the characteristic vocalisation peak of a particular species, an obvious one being that there is likely to be a significant degree of *intra*-specific variation in reproductive behaviour (Pechmann *et al.* 1991). Furthermore, many amphibians are known to exhibit marked behavioural responses to the local presence and reproductive activity of other individuals of both the same and other species (e.g. Blair 1961; Ryan *et al.* 1981; Schwartz & Wells 1985). Such natural variability could help explain the differences in patterns of calling activity of a number of species when compared between different ponds (see Species & Site Accounts). This is particularly evident for *A.callidryas* which exhibits almost exactly the same pattern at Puzzle Pond and the Aguada, but far less concordance when observed across other sites (see Figure 5.5). It is possible that the presence of other species at all sites other than Puzzle Pond and the Aguada serves to confound what might otherwise be the archetypal uninterrupted pattern of vocalisation activity for *A.callidryas*. Finally, sampling error, observer bias, and small sample sizes undeniably contribute perhaps what is the greatest proportion of the between site and between night variance in vocalisation patterns. It is relevant to note that an understanding of the temporal partitioning of reproductive activity, which is recognised to be an important isolation mechanism in amphibian communities, may be particularly important in predicting long-term alterations in the strength and nature of biotic interactions following the demise of any one species. For example the reduction or loss of a vocalising species from the community may produce a strong selection pressure on other species to utilise the vacated calling 'space' – thus altering the life time reproductive success of other species, and the overall structure of the community. As emphasised in Chapter 1, amphibians play an integral role in ecosystem dynamics and function, and any such change in structure could bear important and far reaching consequences over wide spatial and temporal scales.

In agreement with the results of this study, it is perhaps unsurprising that some of the most comprehensive ecological studies on amphibian communities have concluded that local biotic and

abiotic environmental variables play little role in determining the diversity and relative abundance of amphibians at any one site (e.g. Gascon 1991; Williams & Hero 2001; but see Pearman 1997). However, a considerable number of studies have reported a significant role of climatic variables in the determination of *temporal* patterns of amphibian activity – notably with rainfall (Blair 1961; Bowker & Bowker 1979; Aichinger 1987; Gascon 1991; Donnelly & Guyer 1994; Pearman 1997). With particular reference to the neotropics, rainfall is considered to be the most important factor regulating amphibian dynamics – both in Central and South America (Bowker & Bowker 1979; Aichinger 1987; Pearman 1997). Although only a preliminary analysis has been made so far, the results of this study suggest that at least some of the species conform to this theory (see Table 5.15). A number of species show a relatively strong positive correlation between both relative abundance (VC) and vocalisation activity and rainfall (e.g. *H.loquax*), although more species show a close correlation only between vocalisation *activity* and rainfall (e.g. *R.berlandieri*, *S.baudinii*). One point that is of particular interest is that those species which show the strongest correlation of activity with rainfall (*H.loquax*, *S.baudinii* and *R.berlandieri*), all do so with respect to the *duration* of rainfall rather than the volume per se. This is particularly relevant in light of recent claims that alterations in regional climatic *patterns* could bear important implications for amphibian populations (see Chapter 1). However, it is clear that a number of species exhibit either no correlation with rainfall, or even significantly negative relationships. Although one could imagine possible mechanisms for such phenomena (i.e. strong negative interactions with species that are positively stimulated by rainfall), it is more likely that many of the results are due to small sample sizes and sampling error. A further problem is one that is prevalent throughout all ecology – that of the appropriate and *ecologically significant* level of resolution in sampling environmental variables to identify patterns and process in natural systems (Gascon 1991; Laurance *et al.* 1996; McCarty 2001; Williams & Hero 2001). Project Anuran intends to conduct a finer scale sampling regime of the appropriate environmental variables during future field phases in order to identify the significant level of integration.

In summary it seems that the spatial arrangement of the vocalising amphibian community at Las Cuevas is determined primarily not by local habitat characteristics, but rather by regional, historical and even stochastic influences. Under our preliminary analysis species do not appear to covary in any obvious groups or assemblages but rather are responding in their distribution to independent environmental requirements, and stochastic processes such as immigration, colonisation and extinction. In this way the amphibian community appears to conform more to Gleason's paradigm

of community ecology rather than the more superorganismic paradigm of Clements. The role of regional over local processes in community ecology has received increasing recognition in recent years (Ricklefs 1987; Ricklefs & Schuller 1993; Huston 1994), with consequently important implications for the monitoring and interpretation of amphibian populations (see Chapter 1).

As discussed in Chapter 1, recognition of the importance of regional processes for amphibian population dynamics emphasises the importance of a regional monitoring perspective. The concurrent assessment of 8 study sites (plus an extra 3-5 to be added during Phase II) will allow for comparisons between population fluctuations at the regional level, versus population fluctuations at the local (site) level. Furthermore, the relatively frequent intra-annual assessment of each study site will provide an insight into the natural levels of temporal variability in population size. A comprehensive consideration of amphibian populations across both temporal and spatial scales is essential to a successful monitoring program, as it allows the separation of real worrying population declines, from natural variability inherent in amphibian populations. Due to the high level of variability in activity of amphibian populations, few species lend themselves to rapid yet thorough sampling (Heyer *et al.* 1994) – a fact which largely explains the deficit of comprehensive amphibian studies in much of the tropics, and especially in the neotropics where so much amphibian diversity is present (Guyer 1990; Pearman *et al.* 1995). Consideration as to the importance of the optimal allocation of time and resources to budget constrained monitoring projects, highlights the importance of understanding temporal peaks of amphibian activity in allowing rapid and reliable site assessments. The results presented in this study identify that it is important to understand not only the seasonal variation in activity, but also the nocturnal variation, in order to confidently assess each species at its temporal peak of activity. Furthermore, aside from logistical efficiency considerations, an understanding of the diversity of reproductive patterns and modes is vital to understand the pattern and organisation of amphibian communities (Donnelly & Guyer 1994). An understanding of community patterns is central in reaching an understanding of the underlying mechanisms (Levin 1992)– and in the context of declining amphibian populations, the underlying stability.

Few ecological conservation projects in developing countries have access to the levels of expertise, money, or time necessary for thorough ecological assessments (Pearman *et al.* 1995). It is our belief that undergraduate projects such as that of Project Anuran have access to all these requirements, and through the collaboration of student communities from countries rich in resources and expertise,

with students from developing countries where so many conservation problems are focused, can a great deal of progress be made. Although this study represents a very preliminary assessment of the amphibian populations at Las Cuevas, the data collected has provided some valuable insights as to their ecology, in addition to providing an excellent baseline against which to compare data collected during future years.

References

- Adams, M.J. (1999) Correlated factors in amphibian decline: Exotic species and habitat change in western Washington. *Journal of Wildlife Management*, **63**, 1162-1171.
- Aichinger, M. (1987) Annual activity patterns of anurans in a seasonal neotropical environment. *Oecologia*, **71**, 583-592.
- Alford, R.A. & Richards, S.J. (1997) Lack of evidence for epidemic disease as an agent in the catastrophic decline of Australian rainforest frogs. *Conservation Biology*, **11**, 1026-1029.
- Alford, R.A. & Richards, S.J. (1999) Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology Systematics*, **30**, 133-165.
- Anzalone, C.R., Kats, L.B. & Gordon, N.S. (1998) Effects of UV-B radiation on embryonic development in *Hyla cadavina*, *Hyla regilla* and *Taricha torosa*. *Conservation Biology*, **12**, 646-653.
- Barinaga, M. (1990) Where have all the Froggies gone ? *Science*, **247**, 1033 – 1034.
- Beebee, T.J.C. (1995) Amphibian breeding and climate. *Nature*, **374**, 219-220.
- Beebee, T.J.C. (1996) Ecology and Conservation of Amphibians. Chapman and Hall.
- Beebee, T.J.C. (1997) Environmental change as a cause of Natterjack Toad (*Bufo calamita*) declines in Britain. *Biological Conservation*, **11**, 87-102.
- Beebee, T.J.C., Flower, R.J., Stevenson, A.L., Patrick, S.T., Appleby, P.C. *et al.* (1990) Decline of the Natterjack Toad (*Bufo calamita*) in Britain. Paleocological evidence for breeding site acidification. *Biological Conservation*, **53**, 1-20.
- Berger, L. Speare, R., Daszak, P., Green, D.E., Cunningham, A.A. *et al.* (1998) Chytridomycosis causes amphibian mortality associated with population decline in the rainforests of Australia and Central America. *Proceedings National Academy Science USA*, **95**, 9031-9036.
- Berven, K.A. (1990) Factors affecting population fluctuations in larval and adult stages of the wood frog (*Rana sylvatica*). *Ecology*, **71**, 1599-1608.
- Bird, N. M. (1998) *Sustaining the Yield: Improved timber harvesting practices in Belize 1992 – 1998*. Natural Resources Institute
- Blair, W.F. (1961) Calling and spawning seasons in a mixed population of anurans. *Ecology*, **42**, 99-110.
- Blaustein, A.R. & Wake, D.B. (1990) Declining Amphibian Populations: A Global Phenomenon ? *Trends in Ecology and Evolution*, **5**, 203 –204.
- Blaustein, A.R., Wake, D.B. & Sousa, W. (1994a) Amphibian Declines : Judging stability, persistence, and susceptibility of local populations to local and global extinctions. *Conservation Biology*, **8**, 60 –71.
- Blaustein, A.R., Hokit, D.G., O'Hara, R.K. & Holt, R.A. (1994b) Pathogenic frogs contribute to amphibian losses in Pacific North-West. *Biological Conservation*, **67**, 251-254.

- Blaustein, A.R., Hoffman, D.D., Hokit, D.G., Kiesecker, J.M., Walls, S.C. & Hays, J.B. (1994c) DNA repair and resistance to solar UV-B in amphibian eggs: a link to population declines. *Proceedings of the National Academy of Sciences USA*, **91**, 1791-1795.
- Blaustein, A.R. & Wake, D.B. (1995) The Puzzle of Declining Amphibian Populations *Scientific American*, **272**, 56 – 61.
- Blaustein, A.R. Hoffman, P.P., Kiesecker, J.M. & Hayes, J.B. (1996) DNA repair activity and resistance to solar UV-B radiation in eggs of red-legged frogs. *Conservation Biology*, **10**, 1398-1402.
- Bowker, R.G. & Bowker, M.H. (1979) Abundance and distribution of anurans in a Kenyan Pond. *Copeia*, 278-285.
- Bridges, C.M. & Semlitsch, R.D. (2000) Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. *Conservation Biology*, **14**, 1490-1499.
- Burton, T.M. & Likens, G.E. (1975) Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia*, 541-546.
- Bury, R.B. (1999). A historical perspective and critique of the declining amphibian crisis. *Wildlife Society Bulletin*, **27**, 1064-1068.
- Campbell, J.A. (1998) *Amphibians and reptiles of Northern Guatemala, the Yucatan and Belize*. University of Oklahoma Press, Norman, OK
- Carey, C. Cohen, N. & Rollins-Smith, C. (1999) Amphibian declines: an immunological perspective. *Developmental and Comparative Immunology*. **23**, 459-472.
- Carr, A. & de Stoll, A.C. (eds.) (1999) *Biological monitoring in the Selva Maya*. US Man & Biosphere Program, Tropical Ecosystem Directorate & WCS. Unpublished
- Chapin, F.S. III., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 234-242.
- Clarke, R.D. (1972) Effect of toe clipping on the survival in Fowler's Toad (*Bufo woodhousei fowleri*). *Copeia*, 182.
- Connell, J.H. & Sousa, W.P. (1983) On the evidence needed to judge ecological stability or persistence. *American Naturalist*, **121**, 789-824.
- Crump, M.L., Hensley, F. & Clark, K. (1992) Apparent Declines of the Golden Toad : Underground or Extinct ? *Copeia*, **2**, 413 – 420.
- Crump, D, Berril, M., Coulson, D. *et al* (1999) Sensitivity of amphibian embryos, tadpoles, and larvae to enhanced UV-B radiation in natural pond conditions. *Canadian Journal of Zoology*, **77**, 1956-1966.

- Cunningham, A.A., Langton, T.E.S., Bennett, P.M., Lewin, J.F., Drury, S.E.N., Gough, R.E., & MacGregor, S.K. (1996) Pathological and microbiological findings from incidents of unusual mortality of the common frog (*Rana temporaria*). *Philosophical Transactions of the Royal Society London B*, **351**, 1539-1557.
- Davidson, C., Schaffer, H.B. & Jennings, M.R. (2001) Declines of the California red-legged frog: Climate, UV-B, habitat, and pesticides hypotheses. *Ecological Applications*, **11**, 464-479.
- Diamond, J.M. (1996) Conservation Biology – A-bombs against amphibians. *Nature*, **383**, 386-387.
- Donnelly, M.A. & Crump, M.L. (1998) Potential effects of climate change on two neotropical amphibian assemblages. *Climate Change*, **39**, 541-561.
- Donnelly, M.A. & Guyer, C. (1994) Patterns of reproduction and habitat use in an assemblage of neotropical hyliid frogs. *Oecologia*, **94**, 291-302.
- Drost, C.A. & Fellers, G.M. (1996) Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. *Conservation Biology*, **10**, 414-425.
- Duellman, W.E. & Trueb, L. (1994) *Biology of Amphibians*. John Hopkins University Press.
- Fellers, G.M. & Drost, C.A. (1993) Disappearance of the cascades frog (*Rana cascade*), at the southern end of its range, California, USA. *Biological Conservation*, **65**, 177-181.
- Fisher, R.N. & Schaffer, H.B. (1996) The decline of amphibians in California's Great Central Valley. *Conservation Biology*, **10**, 1387-1397.
- Fouquette, M.J. (1960) Isolating mechanisms in three sympatric treefrogs in the Canal Zone. *Evolution*, **14**, 484-497.
- Freda, F. & Dunson, W.A. (1985) Field and laboratory studies of ion balance and growth rates of ranid tadpoles chronically exposed to low pH. *Copeia*, 415-423.
- Furley, P.A. (1998) History and Destiny of Middle American Forests: The Inheritors of The Mayan Landscape. *Human Activities and Tropical Rainforests*. (B.K. Maloney ed.), pp. 101 – 132. Kluwer Academic Publishers, Netherlands
- Furley, P.A., Penn, M., Bird, N.M. & Murray, M. (2000) Spatial analysis of microenvironmental change and forest composition in Belize. *GIS and Remote sensing in Biogeography and Ecology*. (Millington, A. & Osborne, P. eds.). Kluwer: New York.
- Gamradt, S.S. & Kats, L.B. (1996) Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology*, **10**, 1155-1162.
- Gascon, C. (1991) Population and community level analysis of species occurrences of Central Amazonian rainforest tadpoles. *Ecology*, **72**, 1731-1746.
- Graham, N.E. (1995) Simulation of recent global temperature trends. *Science*, **267**, 666-671.
- Groombridge, B. & Jenkins, M.D. (2000) *Global biodiversity: Earth's living resources in the 21st Century*. World Conservation Press, Cambridge.

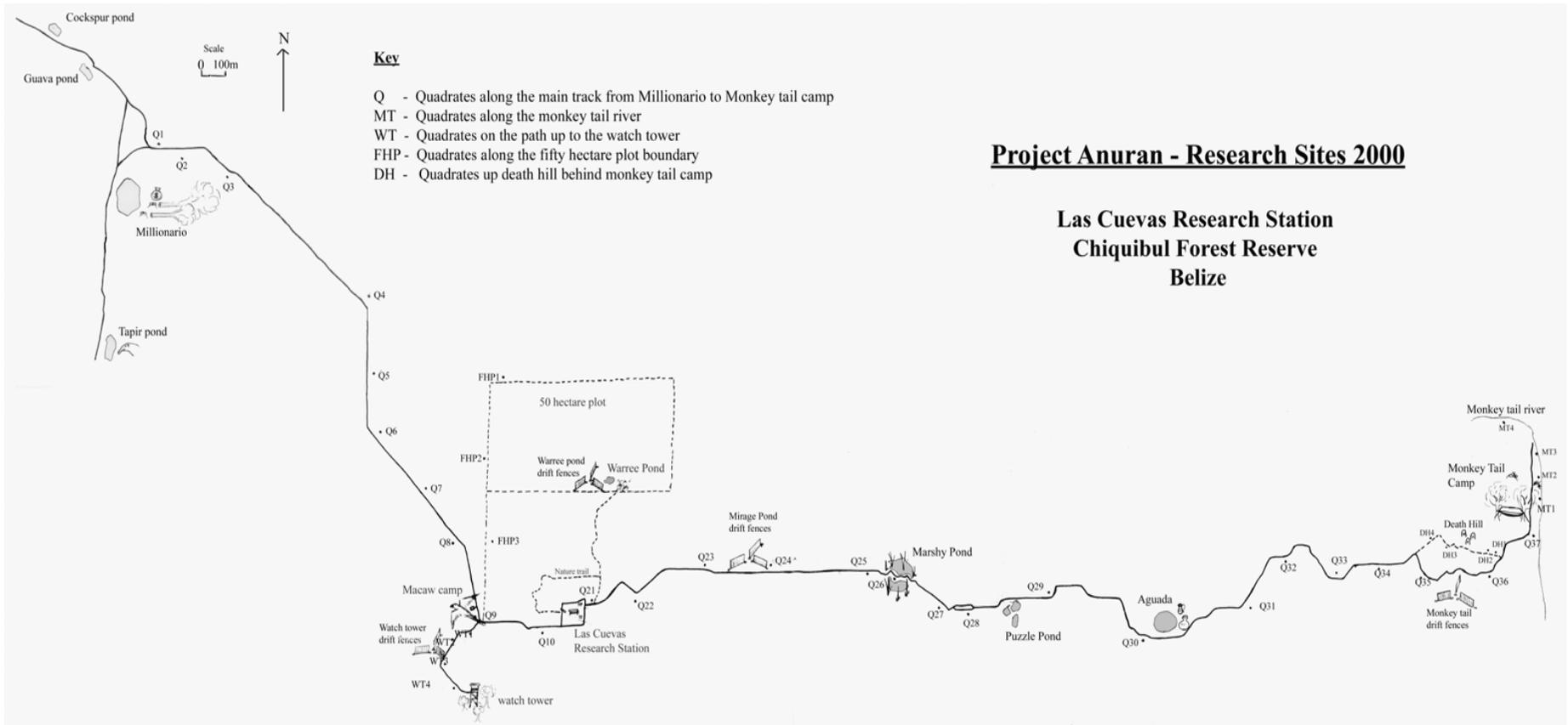
- Guyer, C. (1990) The herpetofauna of La Selva, Costa Rica.. *Four Neotropical Rainforests*. (A.H. Gentry ed.), pp. 371-385. Yale University Press
- Hanski, I. & Gilpin, M.E. (1991) Metapopulation dynamics; brief history and conceptual domain. *Biological Journal Linnaean Society*, **42**, 3-16.
- Harcourt, C. (1996) The conservation Atlas of Tropical Forests of the Americas. IUCN.
- Hartshorn, G. *et al* (1984) *Country Environmental Profile of Belize : A Field Study*. Robert Nicolait & Associates USAID San Jose
- Hayes, J.P. & Steidl, R.J. (1997) Statistical power analysis and amphibian population trends. *Conservation Biology*, **11**, 273-275.
- Hecnar, S.J. & MCloskey, R.T. (1996a) Regional dynamics and the status of amphibians. *Ecology*, **77**, 2091-2097.
- Hecnar, S.J. & MCloskey, R.T. (1996b) The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation*, **79**, 123-131.
- Hero, J.M. & Gillespie, G.R. (1997) Epidemic disease and amphibian declines in Australia. *Conservation Biology*, **11**, 1023-1025.
- Heyer, R.W., Rand, A.S., da Cruz, C.A.G. & Paixoto, O.L. (1988) Decimation, extinctions, and colonisations of frog populations in south-east Brazil and their evolutionary implications. *Biotropica*, **20**, 230-235.
- Heyer, W.R. Donnelly, M.A., McDiarmid, W. Hayek, L.A. & Foster, M.S. (Eds.) (1994) *Measuring and monitoring biological diversity: Standard methods for amphibians*. Smithsonian Institution Press, Washington
- Holmgren, M., Schaffer, M., Ezcurra, E., Gutierrez, J.R. & Mohren, G.M.J. (2001) El Nino effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution*, **16**, 89-94.
- Houlahan, J.E., Findlay, C.S., Schidt, B.R., Meyer, A.H. & Kuzmin, S.L. (2000). Quantitative evidence for global amphibian population declines. *Nature* **404** : 752-755.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56-61.
- Huston, M.A. (1994) *Biological Diversity : The coexistence of species on changing landscapes*. Cambridge University Press
- Inglor, R.F. & Voris, H.R. (1993) A comparison of amphibian communities through time and from place to place in Borean forests. *Journal of Tropical Ecology*, **9**, 409-433.
- IPCC (1995) *Climate Change 1995. Contribution of Working Group I to the 2nd Assessment Report of the Intergovernmental Panel on Climate Change*. University Press, Cambridge.
- Jonsson, M. & Malmqvist, B. (2000) Ecosystem process rate increases with animal species richness: evidence from leaf-eating aquatic insects. *Oikos*, **89**, 519-523.

- Kerr, J.B. & McElroy, C.T. (1993) Evidence for the large upward trends of UV-B radiation linked to ozone depletion. *Science*, **262**, 1032-1034.
- Kiesecker, J.M. & Blaustein, A.R. (1995) Synergism between UV-B radiation and a pathogen magnifies amphibian embryo mortality in nature. *Proceedings of the National Academy of Science USA*, **92**, 11049-11052.
- Kiesecker, J.M. & Blaustein, A.R. (1997) Influences of egg laying behavior on pathogenic infection of amphibian eggs. *Conservation Biology*, **11**, 214-220.
- Kiesecker, J.M. & Blaustein, A.R. (1999) Pathogen reverses competition between larval amphibians. *Ecology*, **80**, 2442-2448.
- Kiesecker, J.M., Blaustein, A.R. & Belden, L.K. (2001) Complex causes of amphibian population declines. *Nature*, **410**, 681-684.
- Laurance, W.F. (1996) Catastrophic declines of Australian rainforest frogs: Is unusual weather responsible? *Biological Conservation*, **77**, 203-212.
- Laurance, W.F., McDonald, K.R. & Speare, R. (1996) Epidemic disease and the catastrophic decline of Australian rain forest frogs. *Conservation Biology*, **10**, 406-413.
- Laurance, W.F., McDonald, K.R. & Speare, R. (1997) In defence of the epidemic disease hypothesis. *Conservation Biology*, **11**, 1030-1034.
- Lawler, S.P., Dritz, D., Strange, T. & Holyoak, M. (1999) Effects of introduced Mosquitofish and Bullfrogs on the threatened California Red-legged frog. *Conservation Biology*, **13**, 613-622.
- Lawton, J.H. (1999) Are there general laws in ecology? *OKIOS*, **84**, 177-192.
- Lee, J.C. (1996) *The amphibians and reptiles of the Yucatan peninsula*. Cornell University Press, Ithaca, London.
- Lee, J.C. (2000) *A field guide of the amphibians and reptiles of the Maya World*. Cornell University Press, Ithaca, London.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* **73**: 1943-1967
- Lips, K.R. (1998) Decline of a tropical montane amphibian fauna. *Conservation Biology*, **12**, 106-117.
- Lips, K.R. (1999) Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology*, **13**, 117-125.
- Long, L.E., Saylor, L.S. & Soule, M.E. (1995) A pH/UV-B synergism in amphibians. *Conservation Biology*, **9**, 1301-1303.
- Loreau, M. (2000) Biodiversity and ecosystem functioning: recent theoretical advances. *Okios*, **91**, 3-17.
- Madronich, S. & Grujii, F.R. (1993) Skin cancer and UV radiation. *Nature*, **366**, 23.

- Marsh, D.M., & Trenham, P.C. (2000) Metapopulation dynamics and amphibian conservation. *Conservation Biology*, **15**, 40-49.
- McArdle, B. & Gaston, K. (1993) The temporal variability of populations. *Oikos*, **67**, 187-191.
- McCarty, J.P. (2001) Ecological consequences of recent climate change. *Conservation Biology*, **15**, 320-331.
- Meyer, A.H., Schmidt, B.R. & Grossenbacher, K. (1998) Analysis of three amphibian populations with quarter-century long time series. *Proceedings of the Royal Society of London Series B*, **265**, 523-528.
- Meyer, J.R. & Foster, C.F. (1996) *A Guide to Frogs and Toads of Belize*. Krieger, Florida
- Meyer J.R., Marlin, J.A. & Arrigoni, J.E. (1999) A proposal to continue and expand the Maya Forest Anuran Monitoring Project in southern Belize. Unpublished Report.
- Meyer, J.R. (1999a) Maya Forest Anuran Monitoring Project (MAYAMON) 1999 Report. Unpublished.
- Meyer, J.R. (1999b) MAYAMON – Maya Forest Anuran Monitoring Project – General information for participants. Unpublished
- Miller, B. & Miller, C. (1995) National protected areas management plan – zoological report : Faunal and site analysis. Unpublished Report.
- Morell, V. (2001) The fragile world of frogs. *National Geographic Magazine*, May, 106-123.
- Naeem, S. Lawler, S.P., Thompson, L.J. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of terrestrial ecosystems. *Nature*, **368**, 734-736.
- Nagle, M.N. & Hofer, R. (1997) Effects of ultraviolet radiation on early larval stages of the Alpine newt, *Triturus alpestris*, under natural and laboratory conditions. *Oecologia*, **110**, 514-519.
- Oldham, R.S. (1974) Mate attraction by vocalization in members of the *Rana pipiens* complex. *Copeia*, 982-984.
- Ovaska, K., Davis, T.M. & Flamarique, I.N. (1997) Hatching success and larval survival of the frogs *Hyla regilla* and *Rana aurora* under ambient and artificially enhanced solar ultraviolet radiation. *Canadian Journal of Zoology*, **75**, 1081-1088.
- Pearman, P.B. (1997) Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology*, **11**, 1211-1225.
- Pearman, P.B., Velasco, M. & Lopez, A. (1995) Tropical amphibian monitoring : A comparison of methods for detecting inter-site variation in species composition. *Herpetologica* **51** 325-335.
- Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J. & Gibbons, J.W. (1991) Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science*, **253**, 892-895.
- Peterman, R.M. (1990) Statistical power analysis can improve fisheries research and management. *Canadian Journal of Fish Aquatic Science*, **47**, 2-15.

- Pounds, J.A. (2001) Climate and amphibian declines. *Nature*, **410**, 639-640.
- Pounds, J.A. & Crump, M.L. (1994) Amphibian declines and climate disturbance : The case of the Golden Toad and the Harlequin Frog. *Conservation Biology*, **8**, 72 – 85.
- Pounds, J.A., Fogden, P.C., Savage, J.M. & Goman, G.C. (1997) Tests of null models for amphibian declines on a tropical mountain. *Conservation Biology*, **11**, 1307-1322.
- Pounds, J.A., Fogden, M.P.L, Campbell, J.H. (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611-615.
- Pyburn, W.F. (1970) Breeding behavior of leaf frogs *Phyllomedusa callidryas* and *Phyllomedusa decicolor* in Mexico. *Copeia*, 209-218.
- Rand, A.S. & Myers, C.W. (1990) The herpetofauna of Barro Colorado Island, Panama : An ecological summary. *Four Neotropical Rainforests*. (A.H. Gentry ed.), pp. 386-409. Yale University Press.
- Reed, J.M. & Blaustein, A.R. (1995) Assessment of ‘non-declining’ amphibian populations using power analysis. *Conservation Biology*, **9**, 1299-1300.
- Resetartis, W.J. & Wilbur, H.M. (1991) Calling site choice by *Hyla chrysoscelis*: effect of predators, competitors, and oviposition sites. *Ecology*, **72**, 778-786.
- Ricklefs, R.E. & Schluter, D. (1993) Species diversity: Regional and historical influences. *Species Diversity in Ecological Communities : Historical and Geographical Perspectives*. (R.E. Ricklefs & D. Schluter. Ed), pp. 350-364. University of Chicago Press
- Ricklefs, R.E. (1987) Community diversity: Relative roles of local and regional processes. *Science*, **235**, 67-171
- Romney D.H, *et al.* (1959) *Land in British Honduras: Report of the British Honduras land-use survey team*. HMSO
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press
- Ryan, M.J., Tuttle, M.D. & Taft, L.K. (1981) The costs and benefits of frog chorusing behaviour. *Behavioural Ecology and Sociobiology*, **8**, 273-278.
- Schwarkopf, L. & Alford, R.A. (1996) Desiccation and shelter-site use in a tropical amphibian: comparing toads with physical models. *Functional Ecology*, **10**, 193-200.
- Schwartz, J.J. & Wells, K.D. (1985) Intra- and Interspecific vocal behaviour of the neotropical treefrog *Hyla microcephala*. *Copeia*, **1**, 27-38.
- Sjogren, P. (1991) Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal Linnaean Society*, **42**, 135-147.
- Stewart, M.M. & Pough, F.H. (1983) Population density of tropical forest frogs: relation to retreat sites. *Science*, **221**, 570-572.

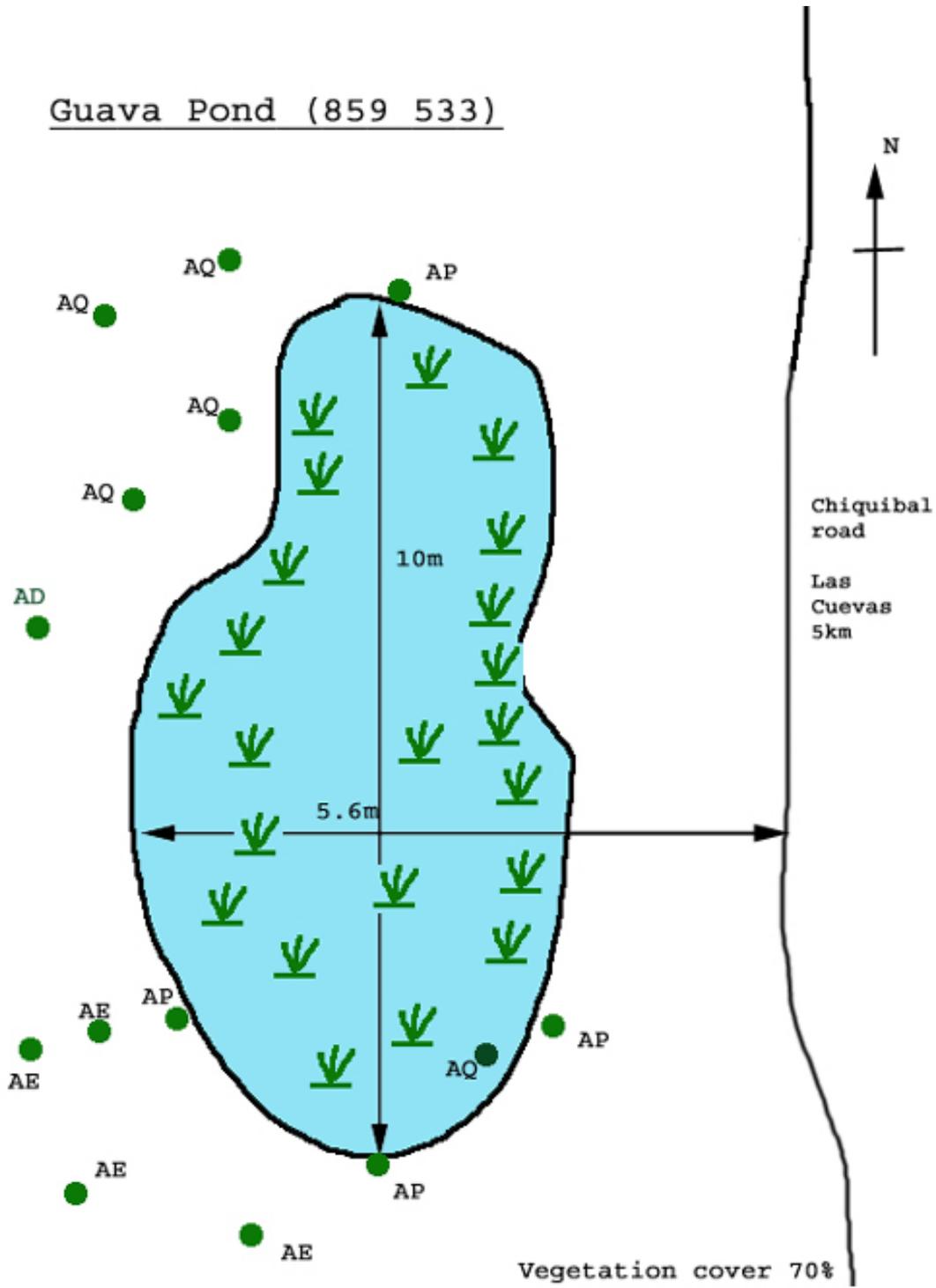
- Still, C.J., Foster, P.N., Schneider, S.H. (1999) Stimulating the effects of climate change on tropical montane cloud forests. *Nature*, **398**, 608-610.
- Thomas, L. (1997) Retrospective power analysis. *Conservation Biology*, **11**, 276-280.
- Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **367**, 363-365.
- Toft, C.A. (1980a) Resource partitioning in amphibians and reptiles. *Copeia*, 1-21
- Toft, C.A. (1980b) Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia*, **45**, 131-145.
- Turner, F.B. (1962) The demography of frogs and toads. *Quaternary Review of Biology*, **37**, 303-314.
- van der Mortel, T., Buttemer, W., Hoffman, P., Hays, J. & Blaustein, A. (1998) A comparison of photolyase activity in 3 Australian treefrogs. *Oecologia*, **115**, 366-369.
- Wake, D.B. (1991) Declining Amphibian Populations. *Science*, **253**, 860.
- Wake, D.B. (1998) Action on Amphibians. *Trends in Ecology and Evolution*. **13**, 379 – 380.
- Wells, K.D. & Schwartz, J.J. (1984) Vocal communication in a neotropical treefrog, *Hyla ebraccata*: advertisement calls. *Animal behaviour*, **32**, 405-420.
- Wells, K.D. (1977) The social behavior of anuran amphibians. *Animal Behavior*, **25**, 666-693.
- Williams, S.E. & Hero, J.M. (1998) Rainforest frogs of the Australian Wet Tropics: guild classification and the ecological similarity of declining species. *Proceedings of the Royal Society of London B Series*, **265**, 597-602.
- Williams, S.E. & Hero, J.M. (2001) Multiple determinants of Australian tropical frog biodiversity. *Biological Conservation*, **98**, 1-10.
- Woolbright, L.L. (1991) The impact of Hurricane Hugo on forest frogs in Puerto Rico. *Biotropica*, **23**, 462-467.



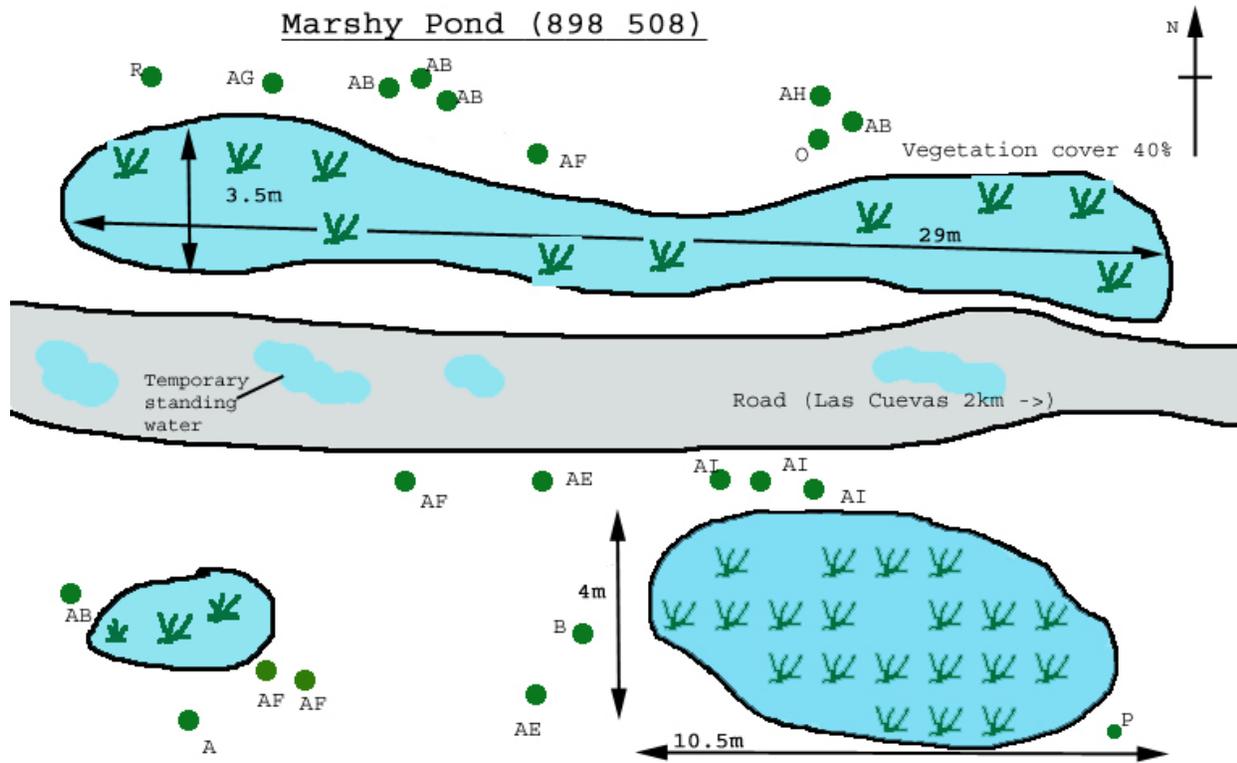
Key to pond vegetation.

A	<i>Terminalea amazonia</i>
B	<i>Trophis racemosa</i>
C	<i>Trichilia moschata</i>
D	<i>Nectandra spp</i>
E	<i>Sabal mauritiiforms</i>
F	<i>Pouteria campechiana</i>
G	<i>Cryosophila stauracantha</i>
H	<i>Pimenta dioica</i>
I	<i>Brosimum alicastrum</i>
J	<i>Dialium guianese</i>
K	<i>Busera simaruba</i>
L	<i>Cedrela odorata</i>
M	<i>Hydrastis canadensis</i>
N	Large ferns
O	<i>Acacia cookii</i>
P	<i>Spondias mombin</i>
Q	<i>Lysiloma acupulcensis</i>
S	<i>Vitex quameri</i>
T	<i>Sebastiania longicuspis</i>
U	<i>Lonchocarpus castilloi</i>
V	<i>Cecropia obtusifolia</i>
X	<i>Bauhinia divaricata</i>
Y	<i>Neurolema lobata</i>
z	<i>Swietenia macrophylla</i>
AA	<i>Attalea cohune</i>
AB	<i>Colophyllum brasiliense</i>
AC	<i>Aspidosperma megalocarpon</i>
AD	<i>Andia inermis</i>
AE	<i>Platymiscium yucatanum</i>
AF	<i>Coccoloba sp.</i>
AG	<i>Dendropanox arboreus</i>
AH	<i>Simarouba glauca</i>
AI	<i>Pseudilmedia spudria</i>
AJ	<i>Licaria</i>
AK	<i>Ficus Sp</i>
AL	<i>Annona squamosa</i>
AM	<i>Bachis Sp</i>
AN	<i>Crescentia cujete</i>
AO	<i>Psidium guaiava</i>
AP	<i>Psidium sartorianum</i>
AQ	<i>Cordia alliodora</i>

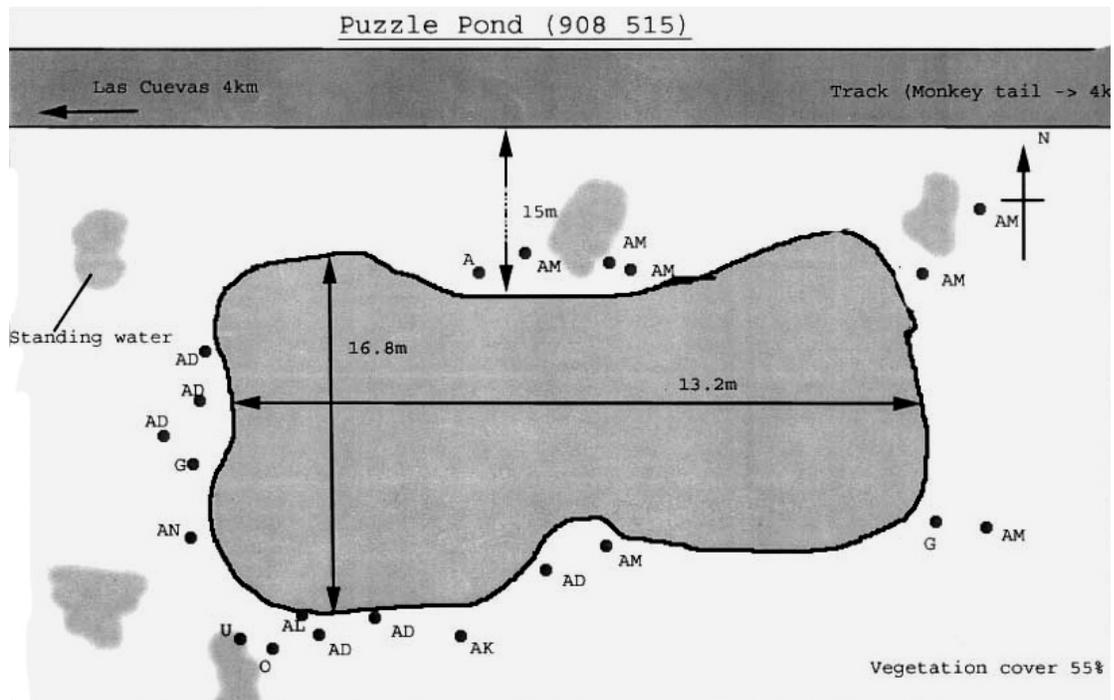
Appendix 2: Guave Pond



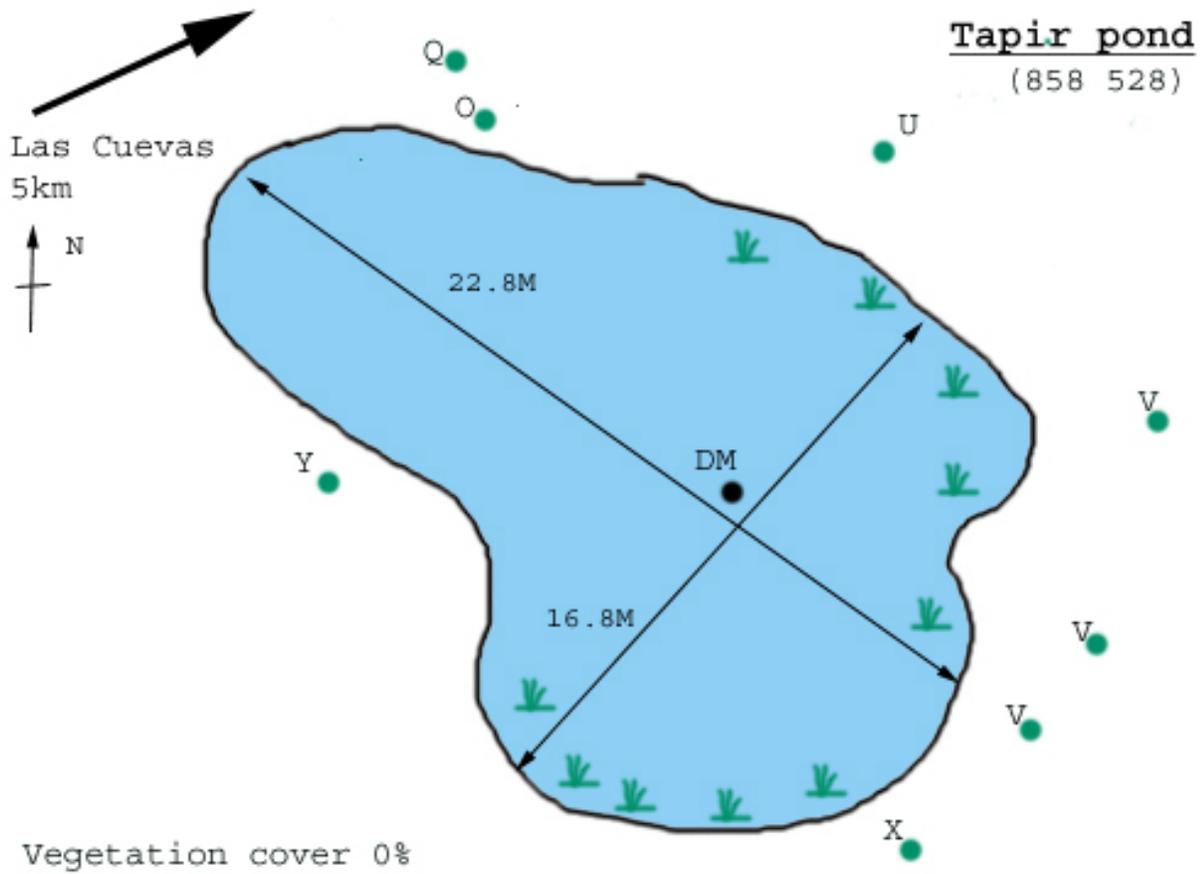
Appendix 2: Marshy Pond



Appendix 2: Puzzle Pond

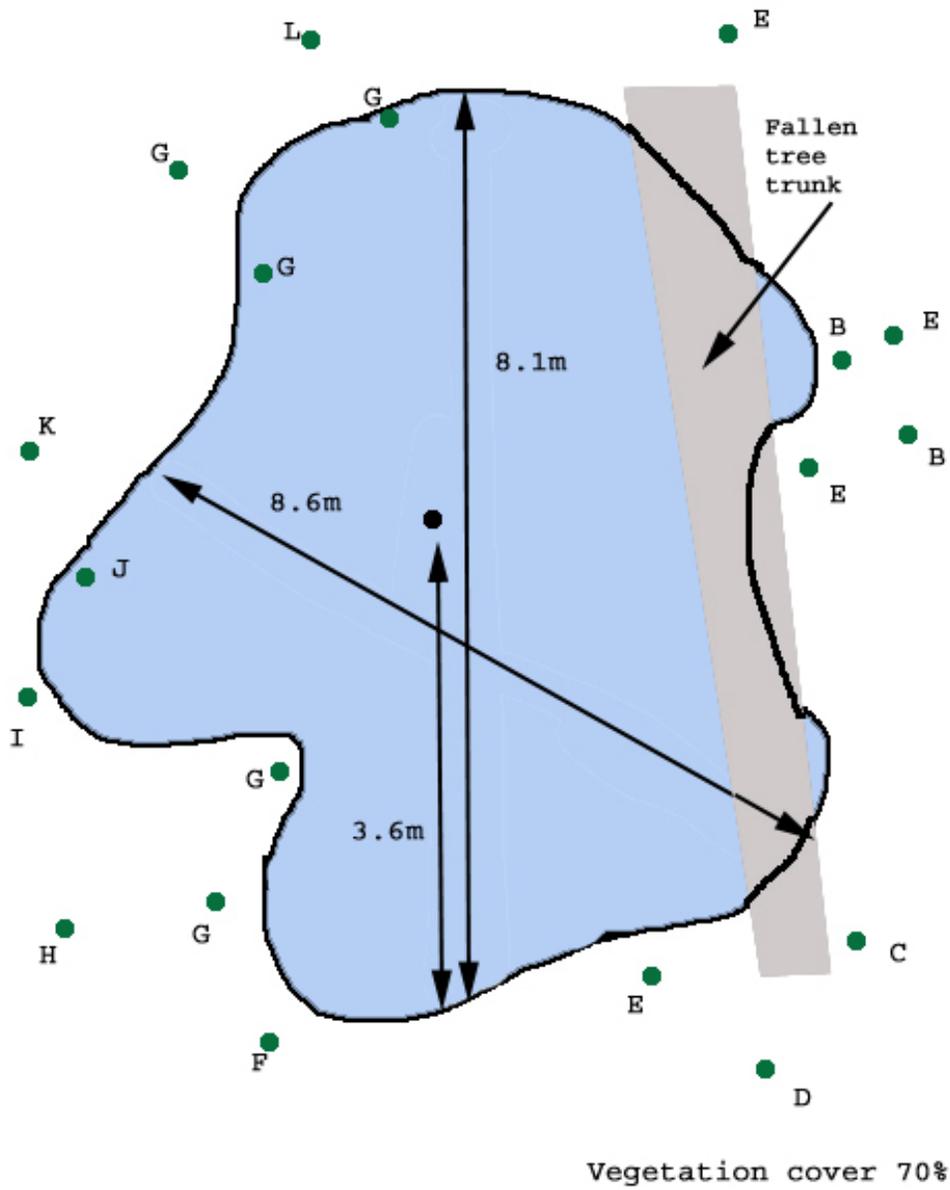


Appendix 2: Tapir Pond



Appendix 2: Warree Pond

Warree Pond (883 515)



Appendix 3 : Marshy Pond

TIME	<i>H. Picta</i>	<i>B. valliceps</i>	<i>H. microcephala</i>	<i>H. ebraccata</i>	<i>G. elegans</i>	<i>A. callidryas</i>	<i>H. loquax</i>	<i>S. baudinii</i>	Water pH	Conductivity (mS/cm)	Rainfall (mm)	Rel. humidity	VPD	Air temperature (oC)	Water temperature (oC)	
MARSHY Pond																
21st July 2000	19:00	2,5	1,2	2,6	2,6	1,2	1,3	1,3	6.32	0.82	0	100	0	22.5	22.5	
Pond depth: N/A	20:00	2,7	1,3	2,7	2,7	1,2	1,4	1,2	6.32	0.82	0	98.676	0.03	21.5	22	
Rainfall: 2hrs 40	21:00	2,7	1,1	2,7	2,7	1,2		1,1	6.32	0.82	0	98.635	0.03	21	21	
Max & Min temp: 22.5, 19	22:00	2,5	1,1	2,5	2,5	1,1	1,2		6.32	0.82	0	98.592	0.03	20.5	21	
Surveyors; Lorry & Nick	23:00	2,7		1,4	1,4	1,3	1,2	1,3	1,2	6.32	0.82	0	97.184	0.07	21	21
moonphase:5	00:00	1,6		1,2	1,2	1,1	1,1	1,3		6.32	0.82	45	raining	0.03	21	21
	01:00	1,3		1,5	1,1	1,3	1,1	1,2	1,1	6.32	0.82	30	raining	0.03	21	21
	02:00	1,2		1,4	1,2		1,3	1,2		6.32	0.82	1	raining	0.07	21	21
	03:00			1,2	1,2		1,3			6.32	0.82	40	raining	0	19	21
	04:00	1,2		1,2			1,2	1,2		6.32	0.82	0	97.184	0.07	21	21
	Total hours called	9	4	10	9	10	8									
	Maximum no. calling	2	1	2	2	1	1									
26th July 2000																
Pond depth: N/A	19:00	1,0		1,3	1,5	1,5			6.59	0.51	0	96.149	0.1	23	24.5	
Rainfall: 0	20:00	1,2		2,6	2,6	1,2			6.59	0.51	0	98.716	0.03	21.5	24	
Max & Min temp: 23, 19.5	21:00	1,0		3,6	3,6	1,3	1,2		6.59	0.51	0	97.184	0.07	21	22	
Surveyors; Lorry & Emily	22:00	1,0		3,6	3,6	1,3			6.59	0.51	0	98.548	0.03	20	22	
moonphase:10	23:00			2,6	2,5	0	1,3		6.59	0.51	0	98.548	0.03	20	22	
	00:00			1,3	1,4	1,3			6.59	0.51	0	98.548	0.03	20	22	
	01:00			1,3	1,1	1,2			6.59	0.51	0	98.502	0.03	19.5	21	
	02:00			1,3	1,1	1,3			6.59	0.51	0	97.004	0.07	20	21	
	03:00			1,3		1,1	1,2		6.59	0.51	0	98.592	0.03	20.5	20	

	04:00		1,2		0	1,1	6.59	0.51	0	98.548	0.03	19.5	20
	Total hours called	4	10	8	8	4							
	Maximum no. calling	1	3	3	1	1							
15th August 2000	19:00		1,5	1,5	2,5	1,6	1,2						
Pond depth: N/A	20:00		2,7	1,5	2,5	1,3	1,3	6.81	0	97.585	0.07	23.5	25.5
Rainfall: 0	21:00		3,7	1,4	1,2	1,3	1,2	6.81	0	98.133	0.05	22.75	24.5
Max & Min temp: 23.5, 21	22:00		3,4		1,3		1,2	6.81	0	97.433	0.07	22.5	24.5
Surveyors; Em & Toby	23:00		1,1		1,3		1,3	6.81	0	98.755	0.03	22.5	23.5
moonphase:1	00:00			1,2	1,2		1,3	6.81	0	98.015	0.05	21.75	23
	01:00			1,1			1,1	6.81	0	98.676	0.03	21.5	23
	02:00							6.81	0	98.635	0.03	21	22.5
	02:00												
	Total hours called		5	5	6	3	7						
	Maximum no. calling		3	1	2	1	1						

Appendix 3 : Warree Pond

WARREE POND	TIME	A. callidryas	A. moreletti	S. baudinii	S. cyanostica	Water pH	Conductivity (mS/cm)	Rainfall (mm)	Rel. humidity	VPD	Air temperature (oC)	Water temperature (oC)
13th July 2000	19:00	1	0	1	6.8	0.6	0	94.7	0.13	23	22	
Pond depth: 35cm	20:00	1	0	1	6.8	0.6	0	97.4	0.07	22	21	
Rainfall: 0	21:00	1	1	1	6.8	0.6	0	97.2	0.07	21	21	
Max & Min temp: 23, 19	22:00	1	0	1	6.8	0.6	0	97.1	0.07	20.5	20.5	
Surveyors; Nick & Toby	23:00	1	0	1	6.8	0.6	0	98.5	0.03	20	20.5	
moonphase	00:00	0	0	0	6.8	0.6	0	98.4	0.03	19	20	
	Total hours called	5	1	5								
	Maximum no. calling											
19th July 2000:	19:00	1,4	2,5		6.8	1.1	0	97.4	0.07	22.5	22	

Pond depth:	20:00	1,5	2,6	6.8	1.1	0	98.7	0.03	21.5	21
Rainfall: 0	21:00	1,3	2,5	6.8	1.1	0	97.3	0.07	21.5	21
Max & Min temp: 23, 19	22:00	0	2,5	6.8	1.1	0	97.3	0.07	21	21
Surveyors; Lorry & Emily	23:00	0	2,4	6.8	1.1	0	96.8	0.07	19	20.5
moonphase 333	00:00	0	1,3	6.8	1.1	0	97	0.07	20	21
	01:00	0	1,2	6.8	1.1	0	95.5	0.1	20.5	21
	02:00	0	1,1	6.8	1.1	0	97	0.07	20	20
	03:00	0	1,3	6.8	1.1	0	97	0.07	20	21
	04:00	0	2,4	6.8	1.1	0	98.5	0.03	19.5	20
	05:00	0	1,3	6.8	1.1	0	98.5	0.03	19	20
Total hours called		3	11							
Maximum no. calling		5	6							
24th July 2000	19:00	1,3	2,4			0	97.5	0.07	23	22
Pond depth:	20:00	1,2	2,2				97.5	0.07	23	22
rainfall: none	21:00	1,2	2,2				98.8	0.03	22.5	21.5
Max & Min temp: 23, 21.5	22:00	1,1	2,2				98.8	0.03	22.5	21.5
Nick, Emily & Mathew	23:00	1,1	1,2				98.1	0.05	22.75	21.5
moonphase : 8	00:00	1,1	1,2				98.7	0.03	22	21.5
	01:00	1,1	1,2				98.7	0.03	21.5	21
	02:00	1,1	1,1				98.6	0.03	21	21
	03:00	0	1,1				98.6	0.03	20.5	21
Total hours called		8	9							
Maximum no. calling		1	2							
15th August 2000										
Pond depth 35 cm	19:00	1,2	1,3	6.78		0	96.1	0.1	23	22
rainfall: none	20:00	1,2	1,3	6.78		0	94.9	0.13	23.5	22
Max & Min temp: 23.5-21.5	21:00	1,2	1,3	6.78		0	97.4	0.07	22	22.5
Nick & Lorry	22:00	1,1	1,2	6.78		0	98.7	0.03	21.5	22
moonphase : 1	23:00	1,1	1,2	6.78		0	98.7	0.03	22	22
	00:00	0	1,2	6.78		0	100	0	21.5	22
	01:00	1,1	1,2	6.78		0	100	0	21.5	22
	02:00	0	0	6.78		0	100	0	21.5	22
Total hours called		6	7							
Maximum no. calling		1	1							

TIME	Species (numbers calling & intensity)					S. baudinii	Water pH	Conductivity. (XXXX)	Rainfall (mm)	Rel. humidity (XXXXX)	VPD=???	Air temperature (oC)	Water temperature (oC)	
	H.loquax	B. valliceps	H. microcephala	R. berlandieri	R. vailanti									H.picta
TAPIR POND														
15th July 2000	19:00	1,4		0	1,1		8.04	6.75	0	93.78	0.165	30	29	
Pond depth: 49cm	20:00	1,5		2,4	1,1		8.04	6.75	0	92.06	0.198	23	28	
Rainfall: 0	21:00	1,6	1,3	2,6	1,2		8.04	6.75	0	98.5	0.3	20	25	
Max & Min temp: 30, 18	22:00	1,6		2,3	1,4		8.04	6.75	10	98.8	0.98	21	25	
Surveyors; Lorry & April	23:00	1,4		0	0	1,1	8.04	6.75	0	93.6	0.132	23	20	
moonphase:27	00:00	1,3		0	0	1,3	8.04	6.75	0	93.6	0.132	23.5	20	
	01:00	1,2			1,5		8.04	6.75	0	98.5	0.033	18	23	
	02:00				1,5	1,2	8.04	6.75	0	98.5	0.033	19	23	
	03:00		1,2	1,3	1,2		8.04	6.75	0	98.5	0.033	19.5	22	
	04:00			1,2	1,1		8.04	6.75	0	96.6	0.066	18	22	
	Total hours called	7	2	5	7	3								
	Maximum no. calling	1	1	2	1	1								
7th August 2000														
Pond depth: 41cm	19:00	1,4	1,5		1,2	1,0	1,1	8.03	0.23	0	96.38	0.10	24	26
Rainfall: 0	20:00	1,4	1,2		1,2	1,6	1,1			0	98.64	0.03	21	26
Max & Min temp: 24,19.5	21:00	1,3			1,2	1,8	1,2			0	98.59	0.03	20.5	26
Surveyors; Lorry & Toby	22:00	1,1	1,2		1,2	1,8				0	97.00	0.07	20	25
moonphase:14	23:00		1,2		1,2	1,7	1,2			0	100.00	0.00	20	25
	00:00				1,2	1,6				0	98.59	0.03	20.5	25
	01:00									0	98.59	0.03	20.5	25
	02:00									0	98.50	0.03	19.5	24

Total hours called	4	4	6	6	4				
Maximum no. calling	1	1	1	1	1				
30th August 2000									
Pond depth: 38cm	19:00	1,5				95.02	0.132	24	27
Rainfall: 0	20:00	1,5				95.78	0.099	21.5	27
Max & Min temp: 24, 21	21:00	1,2				100	0	22	26
Surveyors; Em & Nick	22:00	1,2				100	0	21	26
moonphase:16	23:00					100	0	22	25
	00:00								
	01:00								
	02:00								
Total hours called		4							
Maximum no. calling		1							

Species:number, intensity

		A. callidryas	A. moreletti	R. juliani	H loquax	Water pH	Conductivity. (mS/cm)	Last rain(hr)	Rel. humidity (XXX)	VPD=???	Air temperature (oC)	Water temperature (oC)
AGUADA	TIME											
26th July 200	19:00	2,4	2,3				0.5	0	98.8	0.033	23	22.5
Pond depth: 85 cm	20:00	2,5	2,4				0.5	0	97.4	0.066	22.5	22
Rainfall: 0	21:00	1,4	1,3				0.5	0	98.7	0.033	21.25	22
Max & Min temp: 23, 19.5	22:00	1,3	1,3				0.5	0	98.6	0.033	20.75	21.5
Surveyors; Toby & Nick	23:00	1,2	1,3				0.5	0	97.1	0.066	20.5	21.5
moonphase:10	00:00	1,2	1,2				0.5	0	95.2	0.099	19.5	21
	01:00	1,2	1,2		1,1		0.5	0	98.5	0.033	19.5	20.5
	02:00	1,1	1,1				0.5	0	96.9	0.066	19.5	20
Total hours called		8	8		1							

Maximum no. calling	2	2		1						
22nd august 2000	19:00	1,4	1,2		1,2	6hrs	97.5	0.066	23	22
Pond depth: 69 cm	20:00	2,6	1,2	1,0	1,2		100	0	22	22
rainfall: none	21:00	2,5	1,5				98.7	0.033	21.5	21.5
Max & Min temp: 22, 20	22:00	2,6	1,5				97.2	0.066	21	20.5
Nick, Emily & Lorry	23:00	2,4	1,3				100	0	20	21
moonphase : 8	00:00	1,3	1,2				100	0	20	20
	01:00	1,2	1,1				100	0	20	20
	02:00									
Total hours called		7	7	1	2					
Maximum no. calling		2	1	1	1					
26th August 2000	19:00	2,4	2,7		1,3	26hrs	100	0	22.5	22
Pond depth 75 cm	20:00	2,4	3,7		1,3		98.7	0.033	22	21.5
rainfall: none	21:00	2,4	3,7				100	0	22	22
Max & Min temp: 22,20	22:00	2,5	3,7				100	0	21.5	22
Nick & Lorry	23:00	1,3	2,5		1,1		100	0	21.5	21.5
moonphase : 11	00:00	1,2	2,3				100	0	20	21.5
	01:00	1,2	1,3				100	0	20	20
	02:00	1,2	1,3				100	0	20	20
	03:00	1,1	1,2				100	0	19.5	20
Total hours called		9	9		3					
Maximum no. calling		2	3		1					

TIME	Species, number, intensity					Water pH	Conductivity. (XXXX)	Rainfall (mm)	Rel. humidity (XXX)	VPD=???	Air temperature (oC)	Water temperature (oC)
	<i>B. valliceps</i>	<i>H. microcephala</i>	<i>R. berlanderi</i>	<i>H. loquax</i>	<i>S. baudinii</i>							
Millanario												
14th July 2000	19:00	1,4	0	1,1	1,2	8.16	0.22	0	91.55	0.2	23	30
Pond depth: 62 cm	20:00	2,6	1,2	1,7		8.16	0.22	0	97.18	0.07	21	28
Rainfall: 0	21:00	2,6	0	1,7		8.16	0.22	0	97.1	0.07	20.5	26
Max & Min temp: 23, 17	22:00	1,2	0	1,7		8.16	0.22	0	96.81	0.07	19	26
Surveyors; Emily & Shanna	23:00	1,2	1,1	1,5		8.16	0.22	0	98.45	0.03	18.5	25
moonphase: 27/28	00:00	0	0	1,3		8.16	0.22	0	96.81	0.07	19	24
	01:00	0	0	1,3		8.16	0.22	0	100	0	17	25
	02:00	1,1	0	1,2		8.16	0.22	0	100	0	16.5	24
	03:00	0	0	0		8.16	0.22	0	98.3	0.03	17.5	24
	04:00	1,2	1,2	0		8.16	0.22	0	98.3	0.03	17.5	22
	05:00	1,1	0	0		8.16	0.22	0	96.49	0.07	17.5	25
	Total hours called	8	3	8	1							
	Maximum no. calling	2	1	1	1							
21st July 2000	19:00	1,2	1,5	1,3	2,7	8.03	0.77	0	97.35	0.07	22	22
Pond depth: 71cm	20:00	1,2	1,6	1,2	2,8	8.03	0.77	0	100	0	21	21
Rainfall: 1hr	21:00	2,6	1,5	1,2	2,7	8.03	0.77	0	98.59	0.03	20.5	20.5
Max & Min temp: 22,20	22:00	2,4	1,2	1,5	2,6	8.03	0.77	0	98.55	0.03	20	20
Surveyors; Toby & Emily	23:00	2,4	0	1,6	1,6	8.03	0.77	0	95.55	0.03	20	19.5
moonphase: 5	00:00	1,4	0	1,6	1,5	8.03	0.77	0	95.78	0.1	21.5	19
	01:00	1,2	0	1,5	1,3	8.03	0.77	50	rain	rain	20.5	18.5
	02:00	0	1,3	1,2		8.03	0.77	0	98.64	0.03	21	18
	03:00	0	1,1	1,1		8.03	0.77	0	98.64	0.03	21	18

TIME	Mill	7	4	9	9							
Maximum no. calling		2	1	1	2							
17th august 2000												
Pond depth: 66cm												
Rainfall: 0	19:00				1,4				97.35	0.07	22	24
Max & Min temp: 22, 19	20:00				1,6				98.68	0.03	21.5	25
Surveyors; Lorry & Toby	21:00				1,5				100	0	21	24
moonphase:3	22:00				1,3				98.5	0.03	19.5	24
	23:00			1,1	1,1	1,1			100	0	19	24
	00:00				0							
	01:00				0							
	02:00				0							
Total hours called					1	5	1					
Maximum no. calling					1	1	1					

TIME	Species (numbers calling & intensity)					Water pH	Conductivity. (XXXX)	Rainfall (mm)	Relative humidity (XXXXXX)	VPD=?/?/?	Air temperature (oc)	Water temperature (oc)
	<i>Hyla picta</i>	<i>A callidryas</i>	<i>Hyla microcephala</i>	<i>R berlanderi</i>	<i>H loquax</i>							
Guava Pond												
28th July 2000												
Pond depth: 30cm												
Rainfall: 0	19:00	0	2,5	1,3	2,7	7	0.58	0	98.72	0.033	22	23
Max & Min temp: 22-19.5	20:00	1,3	2,5	2,7	2,7			0	98.64	0.033	21	23
Surveyors; Toby & Nick	21:00	1,4	1,5	3,7	2,6			0	98.55	0.033	20	22
moonphase:12	22:00	1,3	1,5	3,6	1,5			0	100.00	0	19	21
	23:00	1,5	1,2	0	1,4			0	97.10	0.066	20.5	20
	00:00	0	0	0	1,2			0	97.10	0.066	20.5	21
	01:00	0	1,1	1,2	1,1			0	98.64	0.033	21	21

	02:00	0	1,1	1,2		1,1		0	98.50	0.033	19.5	20.5
	Total hours called	4	7	6		8						
	Maximum no. calling	1	2	3		2						
30th July 2000												
	Pond depth: 28cm											
	Rainfall: 0											
	Max & Min temp: 22.5-20											
	Surveyors; Nick & Emily											
	moonphase:14											
	19:00		1,4	1,5	1,1	1,6	7 0.77	0	96.03	0.10	22.5	23.5
	20:00		1,3	1,4	0	1,6		0	97.27	0.07	21.5	23
	21:00		1,3	2,6	0	2,6		0	97.27	0.07	21.5	22.5
	22:00		1,3	2,6	1,1	2,6		0	98.64	0.03	21	22
	23:00		1,2	2,3	1,1	1,3		0	97.89	0.05	20.75	22
	00:00		0	1,2	0	1,2		0	98.59	0.03	20.5	22
	01:00		0	1,2	0	1,1		0	98.55	0.03	20	21
	02:00		0	1,2	0	1,1		0	98.55	0.03	20	20.5
	03:00		0	1,1	0	0		0	98.55	0.03	20	20
	Total hours called		5	9	3	8						
	Maximum no. calling		1	2	1	2						
17th August 2000												
	Pond depth: 48cm											
	Rainfall: 0											
	Max & Min temp: 23.5, 21											
	Surveyors; Em & Nick											
	Moonpahse : 3											
	19:00		1,3	1,4	1,2	0	1,5		98.59	0.033	20.5	22.5
	20:00		1,4	1,4		1,2	1,5		100.00	0	20	22
	21:00		2,6	1,4			1,5		98.55	0.033	20	21.5
	22:00		2,7	1,4	1,2	0	1,5		100.00	0	19.5	21.5
	23:00		1,6	1,3		0	1,5		100.00	0	19.5	21.5
	00:00		1,3	1,2		0	1,4		100.00	0	20.5	21
	01:00		0	1,2		0	1,2		100.00	0	20	21.5
	02:00		0	0		0	0					
	Total hours called		6	7	1	1	7					
	Maximum no. calling		2	1	1	1	1					

TIME	Species (numbers calling & intensity)					H loquax	W ater pH	Conductivity. (XX)	Rainfall (mm)	Rel.humidity (XX)	VPD=???	Air temperature (oC)	Water temp.(oC)
	H. Picta	S bauidini	H. microcephala	R berlanderi	A callidryas								
17th July 2000						1, 1			stor m	rain		21	23
Pondepth: 60 cm Rainfall : 7inches (6-1.30) surveyors: Toby & Shanna Phase of moon: 1	20:00	1, 1				4, 5	1, 1		stor m	rain		21	23
	Total hours called	1				1	1	2					
	Maximum no. calling	1				4	1	1					
24th July 2000	19:00	0	0	2, 3	1, 2	1, 1	1, 3	7.0 0.6 3 4	0	97.58	0.06 6	23.5	26.5
Pond depth: 71cmcm	20:00	1, 3	1, 1	2, 7	1, 2	1, 2	2, 4	7.0 0.6 3 4	0	98.79	0.03 3	23	26
Rainfall: 0	21:00	1, 3	1, 2	2, 7	1, 4	1, 1	1, 2	7.0 0.6 3 4	0	98.79	0.03 3	23	26
Max & Min temp: 23.5-20	22:00	1, 4	1, 2	2, 6	1, 3	0	0	7.0 0.6 3 4	0	98.76	0.03 3	22	25
Surveyors; Toby & Lorry	23:00	2, 7	1, 2	1, 5	1, 4	0	0	7.0 0.6 3 4	0	98.72	0.03 3	22	25
moonphase:8	00:00	1, 3	0	1, 3	1, 6	0	1	7.0 0.6 3 4	0	98.68	0.03 3	21.5	25

	01:00	1, 3	0	1, 2	2, 5	1, 1	0	7.0 3	0.6 4	100.0 0	0.00 0	21	24
	02:00	0	0	1, 2	1, 3	0	0	7.0 3	0.6 4	98.64	0.03 3	21	24
	03:00	0	0	0	0	0	0	7.0 3	0.6 4	98.55	0.03 3	20	24
	Total hours called	6	4	8	8	4	4						
	Maximum no. calling	2	1	3	2	1	2						
28th July 2000	19:00	0		1, 2	0	0	1, 3	7.3 4	1.1 3	98.64	0.03 3	21	24. 5
Pond depth: 61cm	20:00	0		1, 2	0	0	1, 3	7.3 4	1.1 3	98.55	0.03 3	20	24. 5
Rainfall: 0	21:00	0		1, 2	1, 1	0	1, 3	7.3 4	1.1 3	98.50	0.03 3	19. 5	24
Max & Min temp:21-18	22:00	1, 1		1, 2	0	0	1, 3	7.3 4	1.1 3	98.45	0.03 3	19	24
Surveyors; Lorry & Nick	23:00	0		0	0	0	1, 1	7.3 4	1.1 3	98.41	0.03 3	18. 5	24
Moonpahse :12	00:00	0		0	0	0	0	7.3 4	1.1 3	98.50	0.03 3	19. 5	23. 5
	01:00	0		0	0	1, 1	0	7.3 4	1.1 3	100.0 0	0	19. 5	23. 5
	02:00	0		0	0	1, 1	0	7.3 4	1.1 3	98.41	0.03 3	18. 5	22. 5
	Total hours called	1		4	1		5						
	Maximum no. calling	1		1	1		1						

	TIME	Species: number, intensity		H. loquax	Water pH	Conductivity. (mS/cm)	Last rain(hr)	Rel. humidity (XXX)	VPD=???	Air temperature (oc)	Water temperature (oc)
		A. callidryas	A. moreletti								
Puzzle Pond											
22nd August 2000	19:00	2,6	1,4	1,5			6hrs	100	0	22	22
Pond depth: 23cm	20:00	2,6	1,4	1,1				21.5		22	22
rain: TCLR=6hrs	21:00	2,6	1,5					98.7	0.033	21.5	22
Max & Min temp: 22, 19	22:00	2,6	1,5					98.6	0.033	21.5	21.5
Surveyors; Nick & Toby	23:00	1,4	1,4					98.6	0.033	21	21
moonphase : 8	00:00	1,4	1,4					100	0	20.5	21
	01:00	1,2	1,5					100	0	20	21
	02:00	1,2	1,4					100	0	19.5	20.5
	03:00	1,2	1,2					98.5	0.033	19.5	20
	04:00	1,1	1,1					96.9	0.066	19	19.5
	Total hours called	10	10	2							
	Maximum no. calling	2	1	1							
26th August 2000	19:00	2,5	2,6					97.6	0.066	23.5	22.5
Pond depth: 23cm	20:00	3,6	3,6					98.7	0.033	22	22
Rainfall: 0 (26hrs ago)	21:00	2,2	2,5					97.4	0.066	22	22
Max & Min temp: 23.5-20.5	22:00	2,6	2,6					98.7	0.033	21.5	21.5
Surveyors; Toby & Emily	23:00	1,2	1,3					98.7	0.033	21.5	21.5
moonphase:11	00:00	1,3	1,3					100	0	21	21
	01:00	1,2	1,2					97.1	0.066	20.5	20.5
	02:00										
	Total hours called	7	6								
	Maximum no. calling	3	3								

30th August 2000
 Pond depth: 20cm
 rainfall: 0
Max & Min temp: 21.5 - 18
Toby, Lorry and Norry
 moonphase : 16

19:00	1,4	1,4	1,1	1,2	98.8	0.033	23	22.5
20:00	1,4	1,3			98.7	0.033	22	22.5
21:00	1,5	1,3			99.4	0.017	22.25	22
22:00	1,3	1,2			98.7	0.033	22	22
23:00	1,2	1,2			100	0	22	22
00:00	1,2	1,1			98.7	0.033	21.5	22
01:00	1,2	1,1			98	0.05	21.25	21.5
02:00	1,5	1,4			100	0	21	20
Total hours called	8	8	1	1				
Maximum no. calling	1	1	1	2				

TIME	<i>S. stauferi</i>	<i>H. microcephala</i>	<i>R. berlandieri</i>	<i>B. vailliceps</i>	<i>H. picta</i>	<i>S. baudinii</i>	Water pH	Conductivity. (XXXX)	Rainfall (mm)	Rel. humidity (XXXXX)	VPD=???	Air temperature (oc)	Water temperature (oc)
9th August 2000	1,4	1,6	1,4	1,4		0	6.22	0.9	0	96.93	0.0825	23.5	25
Pond depth: 25cm	3,7	2,6	1,5	1,2		1,2	6.22	0.9	0	97.58	0.066	23.5	23.5
Rainfall: 0	3,7	2,6	2,6		1,0	1,2	6.22	0.9	0	98.68	0.033	21.5	23
Max & Min temp: 26,21	3,7	2,5	2,6			1,3	6.22	0.9	0	98.68	0.033	21.5	23
Surveyors; all	3,7	1,5	2,7			1,2	6.22	0.9	0	98.59	0.033	20.5	23
moonphase:24	00:00	2,7	1,4	1,5		1,3	6.22	0.9	0	98.64	0.033	21	22
	01:00	2,6	1,3	1,4		1,3	6.22	0.9	0	98.64	0.033	21	22
	02:00	2,6	1,4	1,2		1,3	6.22	0.9	0	98.68	0.033	21.5	21.5

	03:00	2,6	1,3	1,3		1,3	6.22	0.9	rain	98.68	0.033	21.5	21.5	
	04:00	1,6		0		1,3	6.22	0.9	rain	98.68	0.033	21.5	21.5	
	05:00	1,3		0		1,1	6.22	0.9	rain	97.27	0.066	21.5	22	
	Total hours called	11	9	9		1	10							
	Maximum no. calling	3	2	1		0	1							
13th August 2000														
	Pond depth: 27cm	19:00	1,3	1,4	1,2	1,2	1,1	6.18	0.89	0	98.9	0.033	24.5	26
	Rainfall: 0	20:00	2,5	2,4	0	1,1	1,2	6.18	0.89	0	98.76	0.033	22.5	24
	Max & Min temp: 24.5,21	21:00	3,5	2,5	1,2	1,3	1,3	6.18	0.89	0	96.27	0.099	23.5	24
	Surveyors; Lorry & Em	22:00	3,6	3,5	1,3	1,5	1,3	6.18	0.89	0	98.68	0.033	21.5	24
	moonphase:28	23:00	3,6	2,4	1,2	1,3	0	6.18	0.89	0	98.68	0.033	21.5	23
		00:00	3,6	1,4	0	1,2	0	6.18	0.89	0	100	0	21	22.5
		01:00	1,4	1,2	0	0	0	6.18	0.89	0	98.64	0.033	21	22
		02:00	1,3	0	0	0	0	6.18	0.89	0	98.68	0.033	21.5	22
	Total hours called	8	7	4		6	4							

TREASURY REPORT FOR PROJECT ANURAN Phase I

	<i>Type</i>	<i>Information</i>	<i>Amount (£)</i>
PRE-DEPARTURE	Flights	Mexico City Flight	1,737.67
	Insurance		397.00
	Photographic Equipment and Film		815.67
	Books and Maps		289.60
	Training	First Aid	445.50
		Workshops	380.25
	Vaccinations and antimalarials	Vaccination	175.00
	First Aid Kits		274.15
	Equipment		1,030.37
	Administration		325.55
	Personal and Belizean equipment		698.93
Post expedition	Report printing and distribution	BUDGETED	1,000.00
	Photographic development	BUDGETED	400.00
SUBTOTAL			7,969.69
IN FIELD⁴	Food	NHM - includes batteries and transport to/from Cuevas	2,423.99
	Accomodation	Las Cuevas bill and other in country accomodation	1,177.17
	Research Permit	Included in LCRS bill included in above (£100)	
	In country travel	Before	580.00
		After	180.00
	Flights		432.00
	visas		69.99
SUBTOTAL			4,863.15
TOTAL			12,832.84

⁴ Note that Food, accomodation and travel categories include expenditure of contingency funds during our enforced period of departure