Title Page

FARNBOROUGH COLLEGE OF TECHNOLOGY
SCHOOL OF APPLIED AND HEALTH SCIENCES

**ENVIRONMENTAL INFLUENCES ON THE POPULATION ECOLOGY OF
SIXTEEN ANURAN AMPHIBIANS IN A SEASONALLY FLOODED
NEOTROPICAL FOREST**

by

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ABSTRACT

Amphibians are declining globally from climate change, habitat destruction, pollution and disease. In tropical environments deciphering causes of decline is hampered by a lack of population data. In this study, climate, water quality and amphibian population was recorded at Caño Palma Biological Station in Costa Rica over 3 years. Population dynamics were recorded for 16 species of amphibian and the affects of flooding on them determined.

Spearman Rank Correlation, Principal Component Analysis, Multiple Analysis of Variance and Linear Regression were used to investigate climate and flooding. Direct measurements of aqueous pH, conductivity, iron, nitrate, hardness, oxygen, carbon dioxide and salinity were made through periodic inundation. A mark-recapture program for 16 amphibian species collected population data from an area of *Manicaria* swamp forest and a breeding pond in lowland wet forest. Pollock Open Jolly-Seber and Petersen-Schnabel population models estimated amphibian abundance. Canonical Correspondence Analysis (CCA) was used to investigate relationships between climate, water quality and amphibian populations.

Temperature and humidity remained stable. Rainfall data recorded up to 350mm in one 24 hour period. Flooding occurred annually and was governed by rainfall and spring river tides. Water quality of the environments changed little during flooding. CCA results suggested that amphibian abundance was not related to water quality. Salinity and conductivity levels increased but were not toxic. Amphibian populations fluctuated within and between years. Pollock Open Jolly-Seber estimates were completed for *Chaunus marinus*, *Rana vaillanti* and *Oophaga pumilio*. Petersen-Schnabel estimates were completed for *Bufo coniferus*, *O. pumilio*, *Craugastor fitzingeri*, *Craugastor polyptychus* and *Leptodactylus melanonotus*. All populations appeared unchanged across years. *C. marinus*, *R. vaillanti*, *O. pumilio*, *B. coniferus*, *C. fitzingeri*, *C. polyptychus* and *L. melanonotus* adapted to flooding by altering their preferred behaviour and microhabitat. Most amphibians suspended seasonal activity during flooding.

CONTENTS

TITLE PAGE	1
ABSTRACT	2
LIST OF TABLES	9
LIST OF FIGURES	10
LIST OF PLATES	13
ACKNOWLEDGEMENTS.....	15
GLOSSARY.....	17
1.1 ORIENTATION.....	24
1.2 COSTA RICAN BIOGEOGRAPHY	28
1.3 STUDY SITE LOCATION	29
1.4 THE CLIMATE OF COSTA RICA AND CAÑO PALMA	33
1.5 THE ATLANTIC COAST FLOODPLAIN ENVIRONMENT.....	35
1.6 CAÑO PALMA’S HYDROLOGICAL CYCLE.....	37
1.7 CAÑO PALMA’S HABITATS.....	42
1.8 CAÑO PALMA’S BIOLOGICAL STATION.....	44
1.9 CAÑO PALMA’S FOREST	44
1.10 CAÑO PALMA’S FOREST ZONES	50
1.11 COSTA RICAN HERPETOFAUNA.....	54
1.12 CAÑO PALMA’S HERPETOFAUNA	55
1.13 AN INTRODUCTION TO THE AMPHIBIAN SPECIES STUDIED.....	57
1.13.1 Bufonidae	60
1.13.2 Craugastoridae.....	63
1.13.3 Dendrobatidae	68
1.13.4 Hylidae	73
1.13.5 Leptodactylidae	79
1.13.6 Ranidae.....	82
1.13.7 Strabomantidae	84

1.14	THE ECOLOGY OF HERPETOFAUNA IN FLOODPLAIN ENVIRONMENTS	86
1.15	AMPHIBIAN POPULATIONS, ECOLOGY AND GLOBAL DECLINE	89
1.16	TROPICAL AMPHIBIAN DECLINES	90
1.17	ENVIRONMENTAL AFFECTS TO AMPHIBIANS	94
1.17.1	Climate	94
1.17.2	Precipitation	95
1.17.3	Ambient Wind	96
1.17.4	Water Chemical Composition	96
1.17.5	Pollution Risk at Caño Palma	103
1.18	SURVEYING FOR TROPICAL AMPHIBIANS	103
1.18.1	Pond Habitat Niches	104
1.18.2	Forest Habitat Niches	105
1.19	METHODS OF SURVEYING FOR TROPICAL AMPHIBIANS	106
1.19.1	Visual Encounter Surveys (VES)	106
1.19.2	Leaf-Litter Quadrats	107
1.19.3	Trapping Methods	108
1.20	ESTIMATING TROPICAL AMPHIBIAN POPULATIONS	109
1.20.1	Mark-Recapture (M-RC)	109
1.20.3	Toe-clipping	111
1.21	POPULATION MODELLING OF SURVEY RESULTS	112
1.21.1	Choosing a Population Model	113
1.21.2	Closed and Open Populations; the Jolly-Seber Framework	114
1.21.3	Closed and Open Populations; the Robust Pollock Matrix	122
1.22	INVESTIGATING ECOSYSTEM ENVIRONMENTAL EFFECTS ON AMPHIBIAN POPULATIONS	125
1.22.1	Using Multivariate Techniques	126
1.22.2	Ordination Techniques	126
1.22.3	Canonical Correspondence Analysis (CCA)	129
1.22.4	Interpreting CCA Ordination	131
1.23	TROPICAL ENVIRONMENTS AND AMPHIBIAN POPULATION DYNAMICS	133
1.24	AMPHIBIAN DECLINE AT CAÑO PALMA BIOLOGICAL STATION	136

3.0	METHODOLOGY.....	138
3.1	EXPERIMENT 1; INVESTIGATION AND ANALYSIS OF ENVIRONMENTAL PATTERNS AT CAÑO PALMA.....	139
3.1.1	Summary of Experiment 1.....	139
3.1.2	Detail of Climate Data Measurements	139
3.1.3	Hypothesis for Climate Data	141
3.1.4	Detail of Water Quality Measurements.....	142
3.1.5	Hypotheses for Water Quality	147
3.2	EXPERIMENT 2; ANALYSIS OF AMPHIBIAN POPULATIONS FROM MARK-RECAPTURE DATA	149
3.2.1	Summary of Experiment 2.....	149
3.2.2	Detail of Visual Encounter Surveys (VES).....	151
3.2.3	Detail of Leaf-Litter Quadrats	152
3.2.4	Detail of Caño Palma Biological Station Survey	153
3.2.5	Detail of Mark-Recapture Technique.....	154
3.2.6	Detail of Population Modelling Approach	155
3.3	EXPERIMENT 3; INVESTIGATION OF FLOODING, AMPHIBIAN POPULATIONS AND WATER QUALITY RELATIONS	157
3.3.1	Summary of Experiment 3.....	157
3.3.2	Detail of Canonical Correspondence Analysis.....	158
3.3.3	Hypotheses of Canonical Correspondence Analysis.....	159
3.4	COLLECTION OF VOUCHER SPECIMENS	159
4.0	RESULTS	161
4.1	EXPERIMENT 1; INVESTIGATION AND ANALYSIS OF ENVIRONMENTAL PATTERNS AT CAÑO PALMA.....	161
4.1.1	Environment Data; Tests of Hypotheses	161
4.2	EXPERIMENT 2-ANALYSIS OF AMPHIBIAN POPULATIONS FROM MARK-RECAPTURE DATA	181
4.2.1	Caño Palma Biological Station Pond Data.....	181
4.2.2	Caño Palma Forest Species Data.....	194

4.3	EXPERIMENT 3-INVESTIGATION OF FLOODING, AMPHIBIAN POPULATIONS AND WATER QUALITY RELATIONSHIPS	207
4.3	BEHAVIOUR AND ECOLOGICAL OBSERVATIONS	215
5.0	DISCUSSION	216
5.1	EXPERIMENT 1-AN INVESTIGATION AND ANALYSIS OF ENVIRONMENTAL PATTERNS AT CAÑO PALMA.....	216
5.1.1	Caño Palma Environment Data	216
5.1.2	Water Chemistry Data	225
5.2	EXPERIMENT 2-AN ANALYSIS OF AMPHIBIAN POPULATIONS FROM MARK-RECAPTURE DATA	229
5.2.1	Evaluating the Methods Used in Experiment 2	229
5.2.2	The Abundance and Population Data for Caño Palma Biological Station Pond	236
5.2.3	The Abundance and Population Data for Caño Palma Forest.....	238
5.2.4	An Evaluation of Caño Palma's Amphibian Populations	240
5.2.5	Ecology and Behaviour of Caño Palma's Amphibians	245
5.3	EXPERIMENT 3-INVESTIGATION OF FLOODING, AMPHIBIAN POPULATIONS AND WATER QUALITY RELATIONS	262
5.3.1	Canonical Correspondence Analysis Results (CCA)	262
5.3.2	Floodplain and Climate Affects on Herpetofauna at Caño Palma ..	265
6.0	CONCLUSION.....	279
6.1	AIMS AND CONCLUSIONS	279
6.2	SUGGESTIONS FOR FURTHER STUDY	283
7.0	REFERENCES.....	284
	APPENDIX.....	367
1.0	DETAILED LIST OF PLANT SPECIES IN CAÑO PALMA ZONES	367
1.1	List of the most common plants of the Edge Vegetation Zone	367
1.2	List of the most common plants of the Transitional Vegetation Zone ..	368

1.3	List of the most common plants of the <i>Manicaria</i> Vegetation Zone	369
2.0	VOUCHER COLLECTION MADE DURING FIELD WORK.....	371
3.0	HISTORICAL CLIMATE DATA FOR CAÑO PALMA BIOLOGICAL STATION (COLLATED FROM HISTORICAL DATA RECORDED BY LOCAL RESIDENTS AND EX-MANAGERS OF CAÑO PALMA BIOLOGICAL STATION).....	374
4.0	WATER QUALITY DATA	377
4.1	Water quality data recorded during the 2002/03 survey season and flooding cycle. Yellow highlighting indicates period of flooding	377
4.2	Water quality data recorded during the 2003/04 survey season and flooding cycle. Yellow highlighting indicates period of flooding	378
4.3	Water quality data recorded during the 2004/05 survey season and flooding cycle. Yellow highlighting indicates period of flooding	379
5.0	SPEARMAN RANK CORRELATION, PCA AND MANOVA	380
5.1	Spearman Rank Correlation, PCA and MANOVA for Water Quality 2002/03.....	380
5.2	Spearman Rank Correlation, PCA and MANOVA for Water Quality 2004/05.....	381
5.3	Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years	382
5.4	Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years	383
5.5	Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years	384
6.0	JOLLY-SEBER OPEN POPULATION ANALYSIS.....	385
6.1	Table showing raw Jolly-Seber Open Population analysis for 2002/03 <i>Chaunus marinus</i> capture history data (Not. Def. indicates a no model fit).....	385
6.2	Table showing raw Jolly-Seber Open Population analysis for 2003/04 <i>Chaunus marinus</i> capture history data (Not. Def. indicates a no model fit).....	387

6.3	Table showing raw Jolly-Seber Open Population analysis for 2004/05 <i>Chaunus marinus</i> capture history data (Not. Def. indicates a no model fit).....	389
6.4	Table showing raw Jolly-Seber Open Population analysis for 2002/03 <i>Rana vaillanti</i> capture history data (Not. Def. indicates a no model fit)	392
6.5	Table showing raw Jolly-Seber Open Population analysis for 2003/04 <i>Rana vaillanti</i> capture history data (Not. Def. indicates a no model fit) .	394
6.6	Table showing raw Jolly-Seber Open Population analysis for 2004/05 <i>Rana vaillanti</i> capture history data (Not. Def. indicates a no model fit)	396
7.0	RAW CORRELATING COMPONENTS FOR OUTPUT COMPUTATION OF CCA FOR <i>CHAUNUS MARINUS</i> AND <i>RANA VAILLANTI</i>	399
8.0	SUCCESSFUL RAW OUTPUT COMPUTATION OF CCA FOR <i>CHAUNUS MARINUS</i> AND <i>RANA VAILLANTI</i>	400
9.0	TORTUGUERO AREA HERPETOFAUNA LIST; REVISED 2009	401
10.0	ENVIRONMENTAL VARIABLES MEASURED FOR EACH UNIT - CCA GRAPH FROM GRANT (2005).....	405
11.0	CHECKLIST OF ODONATA IN THE KOEGELBERG RESERVE – SPECIES CODES FOR CCA PLOT FROM GRANT (2005).....	406
12.0	SUCCESSFUL RECOVERY MATRICIES OUTPUT COMPUTATION OF JOLLY-SEBER FOR <i>CHAUNUS MARINUS</i> 2002/03 (TABLE 12.1) AND <i>RANA VAILLANTI</i> 2002/03 (TABLE 12.2).....	407

LIST OF TABLES

Table 1.12.1 Caño Palma Biological Station herpetofauna list.....	56
Table 1.13.1 Species studied; breeding strategy, diel habits and habitat.....	59
Table 1.16.1 Status and literature of neotropical declines.....	91
Table 1.21.2 Modern closed population methods.....	119
Table 4.1.1 Mean Electronic Morning Temperatures (EMT) and Mean Electronic Afternoon Temperatures (EAT) across years.....	161
Table 4.1.2 Mean Rainfall and Total Rainfall across years.....	163
Table 4.1.3 Kruskal Wallace Test results for variation among years of water quality variables.....	171
Table 4.2.1 <i>Chaunus marinus</i> abundance data totals across years.....	182
Table 4.2.2 <i>Rana vaillanti</i> abundance data totals across years.....	182
Table 4.2.3 <i>Chaunus marinus</i> count data totals across years.....	182
Table 4.2.4 <i>Rana vaillanti</i> count data totals across years.....	182
Table 4.2.5 Summary of survey effort for forest amphibian species through sampling years.....	195
Table 4.2.6 Complete abundance (Ni) forest data for forest amphibian species through sampling years.....	198
Table 4.2.7 Numbers of newly marked (Mi) and unmarked but sighted/miss-captured (mi) forest amphibians through sampling years.....	199
Table 4.2.8 Numbers of recaptured (Ni) and inter-year (intNi) recaptured forest amphibians through sampling years.....	200
Table 4.2.9 Pollock Open Jolly-Seber population estimates (JS) from best estimates and indicative Peterson-Schnabel estimates (PS) for forest amphibians that were recaptured through sampling years.....	205
Table 4.2.10 Complete abundance data (Ni) compared against Peterson-Schnabel estimates (PS) for forest amphibians that were recaptured through sampling years.....	206
Table 5.1.2 Saline content of natural water categories.....	226

LIST OF FIGURES

Figure 1.1.1 Location of Costa Rica in the New World.....	24
Figure 1.1.2 Costa Rica's location in Central America.....	25
Figure 1.1.3 Costa Rica's inland mountain ranges.....	26
Figure 1.1.4 Costa Rica's provincial zones.....	26
Figure 1.1.5 Geographical satellite map of northeast Costa Rica.....	27
Figure 1.3.1 Costa Rica's major towns and cities.....	29
Figure 1.3.2 The Tortuguero region's river network.....	30
Figure 1.3.3 Lithograph showing the approximate location of Caño Palma....	31
Figure 1.3.4 Holdridge's (1967) lifezones.....	32
Figure 1.4.1 Regular annual patterns of rainfall across Costa Rica and Central America.....	34
Figure 1.5.1 Major physiography of the Caribbean lowlands of Costa Rica....	36
Figure 1.7.1 Holdridge's lifezones mapped for Costa Rica.....	42
Figure 1.8.1 Layout diagram of Caño Palma Biological Station grounds.....	45
Figure 1.9.1 Caño Palma Biological Station forest showing trails, transects (T1, T2 and T3 respectively), and <i>Manicaria</i> and edge zones, to scale.....	48
Figure 1.22.4 Diagrammatic example of a CCA biplot.....	132
Figure 4.1.1 Mean of morning (M-ET) and afternoon (A-ET) electronic temperatures (°C).....	165
Figure 4.1.2 Mean% relative humidity (RH) recorded using electronic equipment.....	166
Figure 4.1.3 2002/03 annual morning and afternoon precipitation (M-Prec. & A- Prec.) (mm); and water level fluctuation (Check) (mm).....	167
Figure 4.1.4 2003/04 annual morning and afternoon precipitation (M-Prec. & A- Prec.) (mm); and water level fluctuation (Check) (mm).....	168
Figure 4.1.5 2004/05 annual morning and afternoon precipitation (M-Prec. & A- Prec.) (mm); and water level fluctuation (Check) (mm).....	169
Figure 4.1.6 pH levels of all sample year periods.....	173
Figure 4.1.7 Conductivity levels of all sample year periods (mS/mho).....	174
Figure 4.1.8 Hardness levels of all sample year periods (dHmg/l).....	175

Figure 4.1.9 Oxygen levels of all sample year periods (mg/l or ppm).....	176
Figure 4.1.10 Carbon Dioxide levels of all sample year periods (mg/l or ppm)	177
Figure 4.1.11 Salinity levels of all sample year periods (ppt).....	178
Figure 4.1.12 Regression plot of salinity and water levels for 2002/03 water quality data that successfully correlated by Spearman Rank Correlation.....	179
Figure 4.1.13 Regression plot of pH and water levels for 2004/05 water quality data that successfully correlated by Spearman Rank Correlation.....	180
Figure 4.2.1 Population estimates of <i>Chaunus marinus</i> over sampling days for 2002/03; using Pollock Open Jolly-Seber model.....	185
Figure 4.2.2 Captures + capture additions of <i>Chaunus marinus</i> over sampling days for 2002/03; using Pollock Open Jolly-Seber model.....	186
Figure 4.2.3 Population estimates of <i>Chaunus marinus</i> over sampling days for 2004/05; using Pollock Open Jolly-Seber model.....	187
Figure 4.2.4 Captures + capture additions of <i>Chaunus marinus</i> over sampling days for 2004/05; using Pollock Open Jolly-Seber model.....	188
Figure 4.2.5 Population estimates of <i>Rana vaillanti</i> over sampling days for 2002/03; using Pollock Open Jolly-Seber model.....	189
Figure 4.2.6 Captures + capture additions of <i>Rana vaillanti</i> over sampling days for 2002/03; using Pollock Open Jolly-Seber model.....	190
Figure 4.2.7 Population estimates of <i>Rana vaillanti</i> over sampling days for 2003/04; using Pollock Open Jolly-Seber model.....	191
Figure 4.2.8 Captures + capture additions of <i>Rana vaillanti</i> over sampling days for 2003/04; using Pollock Open Jolly-Seber model.....	192
Figure 4.2.9 Graphical visualisation of variance in population estimates to show mean population levels for <i>Chaunus marinus</i>	193
Figure 4.2.10 Graphical visualisation of variance in population estimates to show mean population levels for <i>Rana vaillanti</i>	193
Figure 4.2.11a and 4.2.11b Total abundance (Ni) forest data for forest amphibian species at Caño Palma and from La Selva (Scott (1976))......	197
Figure 4.2.12 Percentage species composition of total sampling years.....	201
Figure 4.2.13 Graph showing skewed distribution population estimates that failed to adequately determine a strong mean in data for <i>Oophaga pumilio</i>	201

Figure 4.2.14 Population estimates of <i>Oophaga pumilio</i> over sampling days for 2003/04; using Pollock Open Jolly-Seber model.....	202
Figure 4.2.15 Captures + capture additions of <i>Oophaga pumilio</i> over sampling days for 2003/04; using Pollock Open Jolly-Seber model.....	203
Figure 4.2.16 Captures + capture additions of <i>Leptodactylus melanonotus</i> over sampling days for 2003/04; using Pollock Open Jolly-Seber model.....	204
Figure 4.2.17 Proportional Abundance of Caño Palma and La Selva Biological Station Compared Total Populations.....	205
Figure 4.3.1 Canonical Correspondence Analysis (2002/03); ordination plot of <i>Rana vaillanti</i> and <i>Chaunus marinus</i> with water quality variables.....	209
Figure 4.3.2 Canonical Correspondence Analysis (2003/04); ordination plot of <i>Rana vaillanti</i> and <i>Chaunus marinus</i> with water quality variables.....	210
Figure 4.3.3 Canonical Correspondence Analysis (2004/05); ordination plot of <i>Rana vaillanti</i> and <i>Chaunus marinus</i> with water quality variables.....	211
Figure 4.3.4 Canonical Correspondence Analysis (2004/05); ordination plot of <i>Rana vaillanti</i> and <i>Chaunus marinus</i> with water levels.....	212
Figure 4.3.5 2003/04 regression of numbers of <i>Chaunus marinus</i> with water levels.....	213
Figure 4.3.6 2004/05 regression of numbers of <i>Chaunus marinus</i> with water levels.....	214

LIST OF PLATES

Plate 1.6.1 Water levels around Caño Palma Biological Station's dock (2002)	39
Plate 1.6.2 Water level during flooding around the same boat dock (2002).....	39
Plate 1.6.3 Dry Biological Station grounds (2002).....	40
Plate 1.6.4 Flooded Biological Station grounds (2002).....	40
Plate 1.6.5 Flooded Biological Station grounds and boat dock (2002).....	41
Plate 1.6.6 Dry Biological Station grounds and boat dock (2004).....	41
Plate 1.7.1 The Caño Palma; bordered by <i>Manicaria</i> swamp forest.....	43
Plate 1.8.1 Caño Palma's main living room within the grounds.....	45
Plate 1.8.2 Caño Palma's lodging facilities.....	46
Plate 1.8.3 Caño Palma Biological Station's permanent pond.....	46
Plate 1.9.1 Typical <i>Manicaria</i> palm swamp forest at the northern end of Caño Palma's forest.....	49
Plate 1.10.1 Area A exhibiting middle sized and hardwood tree species.....	52
Plate 1.10.2 Area B exhibiting sunlight penetration and a shallow temporary pool.....	52
Plate 1.10.3 Area C exhibiting sparse understorey with <i>Manicaria saccifera</i> palm.....	53
Plate 1.13.1.1a Juvenile <i>Bufo coniferus</i>	61
Plate 1.13.1.1b An adult <i>Bufo coniferus</i> on <i>Manicaria saccifera</i> leaf.....	61
Plate 1.13.2 An adult male <i>Chaunus marinus</i> calling from a hammock at the Biological Station pond	62
Plate 1.13.2.1 Adult <i>Craugastor fitzingeri</i>	65
Plate 1.13.2.2 Juvenile <i>Craugastor noblei</i> among leaf-litter.....	65
Plate 1.13.2.3a An adult <i>Craugastor polyptychus</i> on leaf-litter in deep forest.....	67
Plate 1.13.2.3b An adult <i>Craugastor polyptychus</i> on leaf-litter.....	67
Plate 1.13.3.1 Adult <i>Oophaga pumilio</i>	70
Plate 1.13.3.1b An adult <i>Oophaga pumilio</i> climbing young understorey tree in forest.....	70

Plate 1.13.3.1c An <i>Oophaga pumilio</i> tadpole in a rain-filled <i>Guzmania</i> sp. bromeliad.....	72
Plate 1.13.4.1 An adult <i>Agalychnis callidryas</i> perched on a <i>Costus</i> sp. florete.....	74
Plate 1.13.4.2 An adult <i>Dendropsophus phlebodes</i> resting on understory leaf.....	75
Plate 1.13.4.3 A green morph adult <i>Hypsiboas rufitellus</i>	77
Plate 1.13.4.4 Adult <i>Scinax elaeochrous</i> on leaf at night.....	77
Plate 1.13.4.5 A typically coloured adult <i>Smilisca baudinii</i> on <i>Heliconia</i> sp. leaf.....	79
Plate 1.13.5.1 An adult <i>Leptodactylus melanonotus</i> in a pool.....	81
Plate 1.13.5.2 An adult <i>Leptodactylus pentadactylus</i> on <i>Heliconia</i> sp, leaf.....	81
Plate 1.13.6.1a Adult <i>Rana vaillanti</i>	83
Plate 1.13.6.1b An adult <i>Rana vaillanti</i> in pool.....	83
Plate 1.13.7.1 An adult <i>Pristimantis diastema</i> on a leaf at night.....	85
Plate 1.20.1.1 Secure handling of <i>Chaunus marinus</i>	111
Plate 5.2.5.1a Caño Palma Biological Station grounds pond before flooding...	246
Plate 5.2.5.1b Caño Palma Biological Station grounds pond during flooding...	246
Plate 5.2.5.2 Adult <i>Chaunus marinus</i> with forelimb injury and healed scar tissue, suspected from predatory fish attack.....	259

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Field Journal excerpt, Caño Palma - 21st December 2005

Chest wading in flood water and noisy rain, I reached out to part the stems of a Moraceae plant. A lone Bufo coniferus toad hopped in next to me, calling chirpily and vibrating circles of water around its floating body. I leaned in, outreaching with intent to gently capture. A sudden raucous wash of black water startled me aback. My toad vanished and a spiked, dragon-like tail swirled in the flickering torchlight 'Caiman'.

My field journal will ensure that I continue to actively support the campaign for conserving rainforests and forever appreciate the rich experiences I have had whilst conducting this project. These experiences were made possible by the following people who gave time, thought and favour unconditionally over the past 6 years.

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GLOSSARY

Agonistic (behaviour)	Aggressive or defensive actions, such as fleeing or fighting. Often from species interaction.
Amplexus	The process in which a male frog grasps a female with his front legs for fertilisation while she lays her eggs.
Anticyclone	An area of high atmospheric pressure caused by descending air.
Anuran	Any tailless stout-bodied amphibians with long hind limbs for leaping; semi-aquatic and terrestrial species.
Aquents	The level of poorly drained soil that is stratified and clayey or mucky throughout.
Bio-accumulate	To absorb a toxic substance at a rate greater than that at which the substance is lost.
Bioavailability	A description of the fraction of an administered dose of unchanged drug that reaches the systemic circulation.
Binary (Iron) Compound	A compound containing two different elements (e.g. Sodium Chloride, [NaCl]).
Biome	A climate and geographical area of ecologically similar communities of plants, animals and microorganisms.
Bromeliad	A plant of the Bromeliaceae. A large, often arboreal, canopy dwelling family of the New World tropics.

Conspecific	Two or more individual organisms, populations, or taxa belonging to the same species.
Delta (formation)	A triangular deposit of soil or silt formed wherever a water body empties into a lake, ocean or river.
Density (dependency)	A population of organisms that is affected in size and density by its own kind competing for resources.
Digenetic	A subclass (Digenea) of parasitic flatworms that have developmental stages in an intermediate, mollusc host and an adult stage in a vertebrate.
Ecotone	A transition area between two adjacent ecological communities (ecosystems).
Ectothermic	An organism that controls body temperature through external means.
Ephemeral (water body)	A stream, river, pond, pool or lake that only exists for a few days following precipitation or snowmelt.
Epilimnion	The top-most layer in a thermally stratified lake.
Epizootic	A disease that appears as a new case in an animal population, during a period and at a rate that exceeding what is considered "expected".
Friajes	Friajes are a climate anomaly of Amazonia. They are a seasonal change in wind that causes cold Patagonian air to invade warmer lowland tropical forests.

Gyre	A circular or spiralling form of wind or water.
Hammock	Hammocks are dense stands of hardwood trees that grow on natural rises of only a few inches higher than surrounding marshland. Hammocks are formed over thousands of years rising in a wet area through the deposits of their own decomposing organic material.
Hydromorphic	Relating to, or typical of, a soil that has built up in the presence of excess water.
Hydro-oxides	Hydroxy-oxide is a chemical compound containing oxygen (O), the hydroxyl (OH) anion and another chemical element.
Hydrophytes	Plants which are able to live either in water or in very moist soils.
Hyporheic Zone	The area under, or beside a stream channel or floodplain that contributes water to the stream.
Hyperosmoticity	Of, relating to, or characterized by an increased osmotic pressure (typically higher than the physiological level).
Impoundment Pool	A pool created by damming of a flow of water.
Inguinal (gland)	Any of the superficial lymphatic glands in the groin.
Keratin	Tough, insoluble and fibrous structural proteins. Anatomical examples include skin, hair and nails.
Lentic	Living in or relating to still waters (as lakes or ponds).

Levee	A natural or artificial slope or wall, usually earthen and often parallel to the course of a river. Its purpose is that of a flood bank or stop bank for water overflow.
Littorial	Intertidal areas with both terrestrial and aquatic habitats.
Lotic	Of, or relating to, or living in, actively moving water.
Metachrosis	The power of changing colour at will by the expansion of special pigment cells that are controlled by nerves.
Metapopulation	A group of spatially separated populations of the same species which interact.
Nuptial (pad)	A characteristic of or occurring in the breeding season. Nuptial pads often occur on the thumbs of male anurans assisting grip during amplexus.
Ontogenetic	Of, or relating to, the origin and development (embryonic) of an individual organism.
Oophagous	Egg eating.
Perirheic Zone	A complex mixing zone of surface and hyporheic water.
Photophylic	Growing or functioning best in strong light.
Phytotelmic	From Greek-phytos = plant; telm = pond; plural phytotelmata. An organism that breeds in a simple phytotelm environment.

Plasticity	The degree to which an organism's phenotype is determined by its genotype (Phenotypic Plasticity). It is also used to describe an organism's adaptive range in its environment (Environmental Plasticity).
Polychromatic	Having, exhibiting and/or able to change colour.
Polymorphic	The ability to appear in many forms. Biologically, the possession of multiple alleles of a gene within a population, usually expressing different phenotypes.
Polygynous	Polygyny is a form of polygamy, where a male has more than one recognized female sexual partner.
Polyvalent	Acting against or interacting with more than one kind of agent, antigen, antibody, toxin or micro-organism.
Quaternary	The geologic time period from the end of the Pliocene Epoch, roughly 1.806 million years ago to the present.
Regosols	A type of soil consisting of unconsolidated material from freshly deposited alluvium or sand.
Scansorial	Adapted to an arboreal environment (sometimes both arboreal and terrestrial). Usually by evolved feet.
Sequester	To undergo sequestration by forming a stable compound with an ion; 'The cations were sequestered'.
Stochastic	A factor governed by the laws of probability and containing random elements.

Syntopic	Different species found sharing the same habitat within the same area of a geographic range.
Sympatry	Organisms that live in overlapping geographical areas but that do not interbreed.
Tarsus	The section of the vertebrate foot between the leg and the metatarsus.
Tertiary (iron)	A tertiary compound that has three functional groups (i.e. an -NH [ammonia] or -OH [hydroxide] group attached to it).
Thermocline	An area of water within the water column in which the warmer upper waters are prevented from mixing with those at a deeper level.
Trichome	Fine outgrowths or appendages on a plant. Examples are hairs, scales and papillae.
Tympanum	The membranous external auditory structure of a frog. It is often located behind the eye.
Valence (bi/tri-valent)	The maximum number of hydrogen or chlorine atoms that may combine with an atom of the element under consideration (i.e. iron [Fe]), or with a fragment, or for which an atom of this element can be substituted.
Vicariance	The division of a group of organisms by a geographic barrier that results in new varieties or species.
Xeric	A biome characterized by a dry climate.

1.0 INTRODUCTION

Amphibians are declining across the world because of climate change, habitat destruction, pollution and disease (Alford & Richards 1999; Norris 2007). In tropical environments declines are reaching critical levels and some populations of amphibians are at risk of, or have become, extinct (Pounds & Crump 1994). The causes of disappearing amphibia in the tropics are difficult to elucidate due to a lack of knowledge on baseline amphibian populations and natural cycles that contribute to local population fluctuation (Young *et al.* 2001). Costa Rica, in tropical Central America, has already confronted two amphibian species becoming extinct and continues to suffer in a number of ways with the declining amphibian conundrum (Pounds & Crump 1994).

This study aimed to investigate some of the key aspects that have been attributed to amphibian declines in the tropics at a site called Caño Palma Biological Station, which is situated among lowland tropical wet forest land in Costa Rica. The study comprised of surveys that gathered baseline population data for amphibians at the site and experiments that investigated local climate, hydrology, water quality, and how these environmental parameters interacted with amphibian populations.

Costa Rica was chosen as the country of choice for this study because of its previously extensive biotropical research (Leigh *et al.* 1982; Janzen 1983; Gentry 1990; Whitmore 1990; McDade *et al.* 1994; Kricher 1997; Goldsmith 1998; Boza 1993) and because of the urgency needed to address aspects of declines in its amphibian populations (Young *et al.* 2001).

This introduction uses Costa Rica's past ecological research to outline the geographical and environmental forces that have shaped the ecology of the site investigated by this study. It also includes background information on Caño Palma Biological Station, its climate, hydrology, amphibian fauna, amphibian population dynamics and the techniques used to study amphibian populations.

1.1 Orientation

Costa Rica lies 12° latitude and 80° longitude in Central America. The country covers 51100 km² and has vertical relief from sea level to 3820m (Figure 1.1.1).

Figure 1.1.1 Location of Costa Rica in the New World (Expediciones Tropicales).

The north of the country borders Nicaragua and the south, Panama (Figure 1.1.2). Costa Rica separates the Atlantic and Pacific Oceans at less than 482km long and 280km wide.

Figure 1.1.2 Costa Rica's location in Central America (www.acu.edu).

The Pacific coast has two peninsulas, De Nicoya in the northwest and De Osa to the southwest (Figure 1.1.4). Both peninsulas and the northeast of the country are mostly lowland relief.

Further inland, mountain ranges stretch from northwest across the middle of the country and proceed centrally down to Panama (Figure 1.1.3). These ranges form the backbone of the country and house active and dormant volcanoes. The country is divided into provinces that are characterised by tropical forest and volcanic geology (Figures 1.1.3; 1.1.5). Each province has varied topography, flora and fauna (Janzen 1983; McDade *et al.* 1994).

Figure 1.1.3 Costa Rica's inland mountain ranges (© National Geographic 2002).

Figure 1.1.4 Costa Rica's provincial zones.

Figure 1.1.5 Geographical satellite map of northeast Costa Rica (© Universidad de Costa Rica 2004).

1.2 Costa Rican Biogeography

The geology of Costa Rica is varied and well summarised by Castillo-Muñoz (1983), McDade *et al.* (1994) and Savage (2002). Current theories about its formation are derived from plate tectonic movement (Cox & Hart 1986).

Costa Rica was formed after tectonic separation of the Americas during the late Cretaceous period (138 million years ago [mya]) (Pindell & Barrett 1990) and started life as one of a group of islands scattered between the North and South American land masses (Kerr *et al.* 1999). During the Campanian (83mya) these islands occupied the gap between the North and South American land masses (Pitman *et al.* 1993) and by the mid Miocene (15mya) the Isthmus of Panama emerged in contact with South America. Costa Rica was the final link in the island chain connection, forming between Nicaragua and Panama in the mid Pliocene (2.4mya) (Coates & Obando 1996; Duellman 2001).

Scientist's theories about the Quaternary period (1.8mya before early Pleistocene) suggest that Pleistocene (1.8mya) climate fluctuation that occurred during the bridging of the North and South American land masses created an oscillation of species distribution between the two land masses (Duellman 1982; Haffer 1982), with Costa Rica forming the important gateway of this exchange (Janzen 1983; Duellman 1999). During this period depressions of temperatures as low as 5-6°C ensured that hot and humid lowland forests were not an abundant biome (Campbell & Frailey 1984). This resulted in most of the country developing either montane or upland forest (Campbell & Frailey 1984). Lowland forests formed later than higher elevation forests and this may indicate why montane and upland herpetofauna in Costa Rica has evolved more diverse reproductive modes and ecological habits (Duellman 1999; Ron 2000; Savage 2002).

Over subsequent millennia, Costa Rica's geological formation encouraged many species into specialist guilds by its rapid ascent in elevation. This formation also affected climate patterns within the country, which in turn assisted in the evolution of high levels of species diversity and endemism (Janzen 1983; Duellman 1999; Ron 2000; Savage 2002).

1.3 Study Site Location

This study was conducted at Caño Palma Biological Station, a research facility for tropical biologists located north of the town of Tortuguero. Tortuguero is a small coastal fishing village located near the juncture of the Rio Tortuguero, Laguna Penitencia and Laguna Tortuguero on the northeast Caribbean shores of Puerto Limón province (Figure 1.3.1).

Figure 1.3.1 Costa Rica's major towns and cities (© USA Map).

The Tortuguero estuary empties into the Caribbean Sea nearly fifty miles north of Puerto Limón at 10° 37' N latitude and 83° 33' W longitude. The estuary is formed by the confluence of three rivers; the Rio La Suerte, the Rio Agua Fria and the Rio Sierpe. The rivers adjoin approximately a quarter of a mile inland from the ocean (Figure 1.3.2). Caño Palma Biological Station is situated 8km north of the Tortuguero estuary, to the east of the Rio La Suerte confluence. It is located on a backwater canal called the Caño Palma (Caño = Spanish for canal, Palma = Spanish for Palm) that runs parallel with the sea for most of its length and joins the Caño Palacio (Figure 1.3.3). The Biological Station's land is situated between Tortuguero National Park

(18900ha + 52000ha marine reserve) and the Barra del Colorado Refuge (92000ha) that connects with conserved forested land in Nicaragua. Combined, the areas form the largest area of Atlantic tropical lowland wet forest in Central America (Powell *et al.* 2000).

Figure 1.3.2 The Tortuguero region's river network. Note the Caño Palma in the north of the diagram above Laguna Penitencia (Myers 1990).

Caño Palma Biological Station is owned and managed by the Canadian Organisation for Tropical Education and Rainforest Conservation (COTERC) and was purchased and constructed in 1990. The Biological Station's forest land consists of approximately 40ha of lowland tropical wet rainforest (after Holdridge 1967) (Figure 1.3.4). It is bordered on three sides by rivers and by secondary forest on the remaining side (Figure 1.3.3). A distance of 200m separates the Biological Station from the Caribbean Sea. The nearest road is 100km southeast at Puerto Limón city.

Figure 1.3.3 Lithograph showing the approximate location of Caño Palma; the location of the Rio La Suerte and the Caño Palacio / Caño Palma confluence (© Instituto Geográfico de Costa Rica [IGCR]).

Figure 1.3.4 Holdridge's (1967) lifezones; realised from habitat type and climate gradients.

1.4 The Climate of Costa Rica and Caño Palma

Globally, tropical climates are governed by their location, elevation, proximity to water, ocean currents and lunar cycles (McGregor & Nieuwolt 1998; Malhi & Phillips 2005). These factors produce geographically contrasting climates within low latitudes that can define national and regional weather. The mechanisms that create these contrasting climate characters are governed by ascending masses of air that join at the equator. They are known as the Hadley Cells. These meridional circulating air currents generate tropical trade winds. Where the trade winds meet at the equator a band of cloud emerges. This clouded zone is known as the Intertropical Convergence Zone (ITCZ). The ITCZ's seasonal movements are affected by lunar cycles and therefore tidally controlled by oceanic anticyclone gyres. The warm currents and oceanic flows, combined with a number of other atmospheric wind jet streams (called thermal winds), help to create the warm tropical atmosphere of the low latitudes of neotropical America (Kricher 1997; McGregor & Nieuwolt 1998).

The atmosphere above low latitude, coupled with soils and plant species communities are major factors that determine primary productivity in tropical ecosystems (Hartshorn 1992; Orians *et al.* 1996; McGregor & Nieuwolt 1998; Talling & Lemoalle 1998; Baird & Wilby 1999; Malhi & Phillips 2005). Light and temperature regulate plant growth and determine food availability for animals (Talling & Lemoalle 1998; Baird & Wilby 1999), and when these are coupled with heavy tropical precipitation, aquatic ecosystems are created that fast become major biological regulators (Junk *et al.* 1989; Valett *et al.* 1993; Baird & Wilby 1999).

In the tropics, precipitation is characteristically frequent and sometimes heavy (Kricher 1997; Goldsmith 1998). Tropical precipitation often exhibits seasonal patterns that become more pronounced the further north and south travelled away from the equator (Goldsmith 1998; McGregor & Nieuwolt 1998). Seasonality in tropical rainfall is also observed both regionally and locally within a rainforest lifezone (Holdridge 1967; Ribeiro & Adis 1984; Junk *et al.* 1989; Whitmore 1990; McGregor & Nieuwolt 1998). In most rainforest lifezones, morning precipitation falls as dew around sunrise. Rain can also occur regularly and at an approximate time

daily, depending on season and proximity to mountainous terrain (Janzen 1983; McGregor & Nieuwolt 1998).

Lowland wet rainforest in Costa Rica has a climate characterised by high air humidity and stable air temperatures (Holdridge 1967). Such forest is often damp with dense vegetation, a closed canopy and only occasional broken glades (Leigh *et al.* 1982; Janzen 1983; Goldsmith 1998; Gentry 1990; Whitmore 1990; McDade *et al.* 1994; Kricher 1997).

Figure 1.4.1 Regular annual patterns of rainfall across Costa Rica and Central America (© National Severe Storms Laboratory).

Along the Atlantic coast of Costa Rica, the lowland wet forests are exemplary of their classification and exhibit abundant rivers, streams, permanent and temporary pools that are fed by frequent annual rains (Janzen 1983; McDade *et al.* 1994; Savage 2002). Historically, the Tortuguero region's lowland wet forests have received approximately 5000mm of rainfall annually with temperatures fluctuating from 18-35°C (Hirth 1963; Kelso 1965; UICN/ORCA 1992) (Figure 1.4.1). Tortuguero and

the Caño Palma have locally been considered aseasonal as they do not seem to conform to the customary wet and dry seasons of other lowland wet forests (March-Sept; dry/Sept-Feb; wet; [McDade *et al.* 1994]). They are often affected by sea breezes which create extra rainfall and apparent weather cycles (McGregor & Nieuwolt 1998). At Caño Palma, the heaviest rainfall has previously been recorded between November and January and has been coupled with onshore weather and storms from the Caribbean Sea. Drier months at Caño Palma have fallen between January and September although rain has rarely been absent for more than two weeks (Myers 1990).

1.5 The Atlantic Coast Floodplain Environment

Costa Rica's Atlantic lowland wetlands have Quaternary sedimentary geology. Data on the soils in the east lowland regions have been gathered since 1954 and show the soil structure is of variable and alluvial origin, being derived from deposition during delta formation and coastal regosols (Vásquez Morera 1983).

Land in the Tortuguero region comprises a mix of tropical wet forest terrain, swampy permanent and temporary pools, and estuarine floodplain forest that has a frequently saturated water table (Figure 1.5.1). The floodplains usually possess hydrophytes, slopes of <1.0% (Aquepts), undrained hydromorphic soil and are inundated fully or in part during the growing season (May-November) (Myers 1990; Junk *et al.* 2000). Near the Tortuguero estuary, a large proportion of the land is a floodplain ecotone that extends beyond the general classification of 'lowland tropical wet forest', combining lentic (permanent lakes), lotic (river channels), littoral (mobile land-water boundaries) and aquatic or terrestrial transition zones. These zones become periodically inundated by lateral overflow of water and precipitation (Kelso 1965; Junk *et al.* 1989; Baird & Wilby 1999).

Floodplain ecotones vary in their description depending on elevation, hydrological cycle, nutrient status, vegetation cover, connection to perennial water bodies and anthropogenic use (Junk *et al.* 1989). Where floodplain areas connect with perennial water bodies they can be classified as either river floodplains (e.g. those bordering large Amazonian type rivers) or lake floodplains (e.g. Magdalena and Parana River in

Amazonia). In areas like the Amazon, classification of floodplain or land that is subject to periodic inundation falls into several categories of which the most common are Mangrove, Várzea and Igapó (Sioli 1984; Drago 1989; Kricher 1997; Talling & Lemoalle 1998; Ellison 2004a).

Figure 1.5.1 Major physiography of the Caribbean lowlands of Costa Rica; shaded area indicates terrain subject to catchment zone influence (Myers 1990).

Mangrove is essentially a coastal or estuarine habitat that comprises saline tolerant plant species that act as a barrier to tidal erosion (Warne 2007). They blend away from riparian habitat eventually into solid terrestrial land (*terre firme*), border swamp forest and mixed tropical wet forest. Mangrove is distinguished from other floodplain zones by its tidal influence and proximity to the sea (Kelso 1965; Junk *et al.* 1989;

Klinge *et al.* 1990; Warne 2007). In Costa Rica mangroves are common on the Pacific coast but restricted to coastal pockets on the Caribbean side (Gómez 1986).

Várzea is typically riparian swamp forest land that is fed by nutrient rich, sediment loaded, freshwater (Sioli 1984). It is a dominant feature in much of the lowland Amazon basin (Talling & Lemoalle 1998). It also eventually blends into terre firme and mixed lowland tropical wet forest, although can exist for many kilometres in the Amazon where suitable topography permits extensive growth.

Igapó is similar to Várzea but differs in that the donor water supply is 'blackwater', stained with humic substances and organic materials. It has a clear black appearance, low pH, and is low in suspended solids and ionic nutrient content.

Close to the coast in the Tortuguero region the floodplain may be described as Várzea with very sparse Mangrove that borders mixed *Manicaria* and *Raphia* swamp forest. North, at the Caño Palma and tributaries of Tortuguero national park, the floodplain becomes a series of Várzea pockets, with the majority of wet areas being dominated by palm swamp and riparian wet forest edge. A few kilometres further north at the confluence of the Caño Palma and Caño Palacio the terre firme gives way to an abundance of *Manicaria* swamp forest that dominates the riparian edge of the areas canal systems.

1.6 Caño Palma's Hydrological Cycle

Natural inundation events can be caused by storms, high velocity winds, topography, altered flows, excessive precipitation and groundwater fluctuation (Anderson *et al.* 1996; McGregor & Nieuwolt 1998; Talling & Lemoalle 1998). Sometimes flooding can occur from just one of these modes (monomodal) or a selection of them (polymodal).

Monomodal flood pulses are predictable and hold for long durations. They are characteristic of most large rivers in the tropics and are often caused by surplus water from pronounced rainy seasons, tidal sequences and groundwater flooding (Anderson

et al. 1996; Irion *et al.* 1997; Junk 1997; Mertes 1997; Talling & Lemoalle 1998; Junk *et al.* 2000).

Flooding of smaller tropical rivers or backwaters often show a more polymodal, unpredictable flood pulse, of lower amplitude and shorter duration. Such polymodal flood pulses are usually influenced by local precipitation which can subsequently alter the duration and amplitude of the water level (Junk 1997; Talling & Lemoalle 1998; Junk *et al.* 2000).

In small streams and backwaters, like the Caño Palma, localised heavy rainfall can induce spiky rises in water tables and discharge volumes that are high enough to create flash floods (Myers 1990; Junk 1997; Talling & Lemoalle 1998; Junk *et al.* 2000).

The tidal cycle around the Tortuguero estuary is sequential with that of the nearby southern port of Puerto Limón. It comprises a set of two high tides and two low tides in any 24 hour period (Kelso 1965). It was previously thought that Caño Palma may be influenced by this tidal sequence due to its daily rise and fall in levels, regular changes in flow direction from north to south, and passage into the Caño Palacio (Kelso 1965).

Prior to Kelso's (1965) description the Caño Palma's flooding cycle had not been described although it was thought to be activated in the wetter season when coupled with heavy regional rainfall and tidal flow patterns (D. Loth & P. B.C. Grant *pers. comm.*). The hydrological cycle appeared to mimic the functioning of an Igapó floodplain ecotone and may have been sequentially linked to the Tortuguero estuary (R. Ballard; P. B. C. Grant; D. Loth & T. Mason *pers. comm.*) (Plates 1.6.1-1.6.6).

In recent years the Caño Palma canal has exhibited a more prominent indication of being bi-annual with polymodal floods in the wettest periods of its year (November to December and May) (P. B. C. Grant *pers. comm.*).

**Plate 1.6.1 Typical water level at Caño Palma Biological Station's dock (2002).
Note the water level in reference to the pillar support bar on the dock frame.**

**Plate 1.6.2 Water level during flooding around the same boat dock (2002). Note
the water level in reference to the pillar support bar on the dock frame.**

Plate 1.6.3 Dry Biological Station grounds (2002). Note the position of the white weather station box on stilts.

Plate 1.6.4 Flooded Biological Station grounds (2002). Note the position of the weather station box (different angle from Plate 1.6.3).

Plate 1.6.5 Flooded Biological Station grounds and boat dock (2002).

Plate 1.6.6 Dry Biological Station grounds and boat dock (2004).

1.7 Caño Palma's Habitats

Costa Rica contains 12 ecological lifezones several of which are globally endangered (Holdridge 1967; Janzen 1983) (Figure 1.7.1). Tropical wet, moist and dry forests are the most abundant, with tropical wet forests accounting for 5% (2352km²) of the national territory. Most of Costa Rica's tropical wet forest is found in the Caribbean lowlands (Myers 1990) and typically comprises a combination of palm swamps in saturated high canopy forest.

Figure 1.7.1 Holdridge's lifezones mapped for Costa Rica; purple = lowland tropical wet forest; adapted from Savage (2002) ©.

Globally there are many different palm swamps but essentially only three major types in the neotropics; monospecific, species-rich and seasonal. The Tortuguero and Laguna Penitencia region has three varying monospecific swamps; *Manicaria*, Rain-fed *Raphia* swamp and River-fed *Raphia* swamp (Myers 1990; Ellison 2004a).

Plate 1.7.1 The Caño Palma; bordered by *Manicaria* swamp forest. Note the distinctive tannin-rich blackwater.

These three types of monospecific swamps are seasonally or permanently flooded and support different compositions of mixed dicotyledon and Lepidocaryoid palm species (e.g. *Mauritia*, *Raphia* and *Metroxylon*). The palms survive in topographical depressions and mixed forest on higher wet ground (Myers 1990).

Caño Palma's forests are *Manicaria* swamp (Myers 1990; Ellison 2004a) bounded by the Caño Palma, the Caño Penitencia, and the Cerros de Coronel, and Laguna Samay canals (Plate 1.7.1). These swamps have areas of hammocks with shallow depressions and channels. Some depressions remain as permanent pools and others join or become apparent during inundation.

1.8 Caño Palma's Biological Station

Caño Palma Biological Station was comprised of a set of rustic buildings in-keeping with the character of local housing. A main accommodation building existed centrally with three dormitories, a laboratory, sheltered boat dock and washing facilities located within 10-15m of each other (Figure 1.8.1; Plate 1.8.1-1.8.2).

The grounds of the Biological Station buildings was approximately 0.5ha and bordered on the north, south and west by Caño Palma's forested land, and on the east by the Caño Palma. The grounds contained mostly secondary and edge vegetation that has been allowed to grow naturally around the perimeter. A number of collected varieties of native and foreign plant and shrub were planted within the grounds on small raised flowerbeds.

The grounds between buildings and raised vegetation beds comprised of a fairly regularly mown grass lawn (Figure 1.8.1; Plate 1.8.1). A large stand of bamboo (*Bambusa*) was present along the edge of the canal. Coconut palms were also sparsely present in the grounds. The main focal point of the grounds was a small (approximately 8 x 4m), permanent man made pond (Plate 1.8.3).

The Biological Station pond was ecologically similar to many of the pools within Caño Palma's forest. It contained rich tannin stained water, a few floating water hyacinth (*Eichhornia crassipes*), small native fish species, pond sedges and a few select riparian plant species.

1.9 Caño Palma's Forest

Caño Palma's forest boundary was topographically mapped when it was purchased. Further detailed mapping was instigated after a small network of forest trails were created to gain access for studying the forest. Many of these trails were originally small logging paths used to haul wind fallen timber for small construction duties. Subsequently, parts of them formed access paths for researchers to enter the forest. Other, early paths are now derelict and overgrown.

Figure 1.8.1 Layout diagram of Caño Palma Biological Station grounds.

Plate 1.8.1 Caño Palma's main living room within the grounds. Note the manicured Graminae and planted bed on the right of the path.

Plate 1.8.2 Caño Palma's lodging facilities. Note the edge vegetation behind the cabin blending into Caño Palma's forest.

Plate 1.8.3 Caño Palma Biological Station's permanent pond.

Caño Palma's forest had two existing trail networks, the *Raphia* Trail and the Colubri Trail (Figure 1.9.1). The main access trail to the forest was the *Raphia* Trail. This trail commenced alongside the Caño Palma through defined dicotyledon dominated forest and then circumnavigated most of the forest. The first 500m commenced parallel to the canal and was noticeably drier, more shaded and slightly higher in elevation than other trails in the forest.

Toward the northern end of the property the vegetation changed to predominantly *Manicaria* swamp forest (Plate 1.9.1). This area contained scattered temporary and permanent flood pools. The *Manicaria saccifera* palms became a climax community across the crown of the property where marsh/swamp vegetation flourished. A few dicotyledon tree species were scattered within this area but most had died young from flooding or were shaded out by falling *Manicaria* fronds. When the larger *Manicaria* trunks died they were generally replaced by young shoots or nearby clumps, thus maintaining the shaded cover.

Toward the southwest section the *Raphia* Trail cut through a drier, more shaded, territory and connected with the Colubri Trail toward the Biological Station buildings (Figure 1.9.1). The Colubri Trail was a smaller internal trail that was a similar circular shape to the *Raphia* Trail. It adjoined to a northern loop trail, creating a figure of eight trail shape within the southern half of the property. The Colubri Trail passed through a mixture of glades and broad leaved trees with sparse understorey flora. It was usually dry but was the first trail to flood upon a rising water table.

In 2003 a new trail was cut during exploratory searching of Caño Palma's forest. The Rock Trail extended west, away from the Biological Station, and proceeded into an abundance of *Manicaria* swamp forest. It was a linear trail and therefore had to be walked in reverse to return to the Biological Station. The trail is unique in that at its end is a small volcanic uplift that presents a small hill. It was a newly formed trail and did not form part of this study. As such the trail has not been formally mapped.

Figure 1.9.1 Caño Palma Biological Station forest showing trails and transects (T1, T2 and T3 respectively) cutting through edge (Area A), flooded (Area B) and *Manicaria* (Area C) habitat zones.

Plate 1.9.1 Typical *Manicaria* palm swamp forest at the northern end of Caño Palma's forest.

1.10 Caño Palma's Forest Zones

An understanding of the microhabitats at the study site was deemed important because local maps showed the coastal area around Caño Palma as only a vast expanse of palm swamp forest. This broad spectrum mapping misrepresented the riparian boundary of the site. Distinct local forest classification is important as not all palm swamps are wet or contain contiguous forest diversity (Junk *et al.* 1989; UICN/ORCA 1992; Savitsky *et al.* 1998; Nebel *et al.* 2001). It was also important to determine forest zone because amphibian populations in temperate and tropical forests can be spatially determined by microhabitat type (Pearman 1997; Zampella & Bunnell 2000; Gardner *et al.* 2007b). In tropical forests amphibians often exist in specialist niches that are created by a specific seasonality, climate or lifezone (Savage 2002; Wells 2007). These niches subsequently influence distribution and abundance of amphibians over gradients in precipitation (Duellman 1988; Lee 1993), soil moisture (Friend & Cellier 1990; Vonesh 1998), altitude (Lynch & Duellman 1980; Fauth *et al.* 1989), forest type (Crump 1971; Inger & Colwell 1977) and forest structure (Gascon 1991; Lieberman 1986; Pearman 1997). It is widely recognised that obtaining representative amphibian samples from all microhabitats is necessary to help determine spatial distribution and to understand its influence on amphibians (Caughley 1994; Dupuis *et al.* 1995; Skelly & Meir 1997; Williams & Hero 2001; Guerry & Hunter 2002; Armstrong 2005).

Three distinct vegetation types were identified within Caño Palma's forest (see Plates 1.10.1-1.10.3). Each possessed distinct combinations of permanent pools, vegetative glades, tree fall, trail interference, habitat and vegetative species assemblage (see Appendix 1.1-1.3). A combination of the three areas was chosen for study in order to collect data on amphibian populations across all microhabitats. This also helped to form a homogenous representation of total habitat and resident amphibian fauna. The three areas were identified and named as 'Area A (Edge Vegetation)', 'Area B (Occasional Flooding)' and 'Area C (*Manicaria*)'.

Area A (Plate 1.10.1) exhibited raised mounds with broad leaved species and sparse *Manicaria* swamp forest. It had numerous glades and was bordered to the north and west by Area B type habitat, to the east by the Caño Palma canal and to the south by photophylic plant species and the Biological Station. Edge vegetation represented the

smallest of the three zones, covering a total of 178.5m², which corresponds to 3.6% of the forest area shown on Figure 1.9.1 (the measured area). The edge zone was composed of two layers; an understorey and a sub-canopy or middle sized tree layer. The understorey comprised mostly *Calathea*, *Costus* and *Heliconia* species and other species from the Melastomataceae family.

The sub-canopy layer was filled with middle sized trees such as *Hampea appendiculata*, *Apeiba membranacea* and *Cecropia obtusifolia*. Small trees of the Melastomataceae and Annonaceae such as *Conostegia* sp. *Miconia* sp. were abundant and occasional hardwoods like *Xilopia frutescens*, *Psychotria grandis* and *Simarouba amara* were also present.

Area B (Plate 1.10.2) comprised a blend of species, some of which were also found in Area A, with additional glades. The zone had patches of vegetation that were transitional, where a few species from both Area B and C were represented within it. This floral patchiness gave rise to small islands of vegetation located in the middle of an area that comprised mostly *Manicaria* palm. The zone encompassed 1410.3m² or 28.6% of the measured area of forest and was easily the most diverse due to slightly higher ground that enabled competitive species to grow. The transitional vegetation in this area was characterised by understorey, middle sized trees or sub-canopy and canopy tree species.

The understorey of this zone was dominated by herbaceous species such as *Psychotria glomerulata*, *Psychotria saltatrix* and the vine *Strychnos panamensis*. Young saplings of the trees *Xilopia frutescens*, *Grias cauliflora* and *Sterculia recordiana* were abundant in this area. In the sub-canopy, species such as *Dendropanax arboreus*, *Apeiba membranacea* and *Vismia macrophylla*, were most common. *Zygia inequalis* and *Pachira aquatica* occurred closer to the canal. *Manicaria saccifera* was infrequently found and a few individual *Raphia taedigera* palms were present. Neither palm species were sufficient in number to classify the whole forest as strictly *Raphia* or *Manicaria* palm swamp.

The canopy of Area B was dominated by hardwoods, including *Pentaclethra maculosa*, *Carapa guianensis* and *Symphonia globulifera*.

Plate 1.10.1 Area 'A' exhibiting primarily middle sized hardwood tree species.

Plate 1.10.2 Area 'B' exhibiting sunlight penetration and a temporary pool.

Area C (Plate 1.10.3) (*Manicaria*) comprised mostly *Manicaria* swamp forest with permanent and semi-permanent pools dominated by *Manicaria saccifera* palm. The zone was filled with shade loving understory flora and occupied 3393.3m² or 67.8% of the measured forest area. Area C was less diverse than Areas A and B and characterised by an abundance of naturally high groundwater pools.

**Plate 1.10.3 Area ‘C’ exhibiting sparse understory with
Manicaria saccifera palm.**

Almost monocultural stands of *Manicaria saccifera* dominated Area C's canopy. This domination likely resulted from reduced sunlight reaching the understory, a shorter forest stand height and limited availability of growing space (Henderson 2002). *Psychotria saltatrix* was the most common species among the reduced, spatially open, understory. Saplings of *Grias cauliflora* and *Lacistema aggregatum* were occasionally seen where less saturated soil occurred. The sub-canopy comprised *Malouettia guatemalensis*, *Fassipourea elliptica* and *Garcinia madruno*. The high canopy comprised predominantly *Pentaclethra macroloba*, interspersed with *Carapa guianensis*, *Prioria copaifera*, and *Symphonia globulifera*.

1.11 Costa Rican Herpetofauna

The herpetofauna of Costa Rica is among the best documented of any tropical environment, although the ecology of each species is still far from complete (Young *et al.* 2001). The most studied area is that of La Selva, Heredia Province, where herpetological research has been undertaken since the late 1950's (Donnelly 1994; Guyer 1994; Guyer & Donnelly 2005). The most comprehensive work on the herpetofauna of the country is provided by Jay Savage's book. Savage (2002) summarises much of the known ecology and biogeography of the country's herpetofauna and provides an extensive library of photographs.

Prior to Savage (2002) a number of books with keys, checklists and descriptions were written that covered the classification and distribution of Costa Rican herpetofauna (see Peters *et al.* 1986; Savage & Villa 1986; Günther 1987; Villa *et al.* 1988; Leenders 2001). Other papers that herpetologists relied on were specific in location (Hayes *et al.* 1989; Donnelly 1994; Guyer 1994; Sasa & Solórzano 1995; Stafford 1998; Lewis 2001), had extensive information on specific biological topics such as lifecycle (Lips & Savage 1996a; Köhler & Ziegler 1997) or were restricted to an individual order, family or genus (Savage 1968; Heyer 1970; Starrett & Savage 1973; Harris 1994; Duellman 2001; Solórzano 2005).

Prior to Savage (2002), the most comprehensive key and checklist was Savage & Villa (1986), although many other smaller publications (Solórzano 1993; James *et al.* 1995; Norman 1998) and further descriptive articles assisted in identification and supplemented knowledge on species ecology. A useful selection of publications by Taylor (1951; 1952a-b; 1954a-c; 1956; 1958) provided good descriptions of many reptiles and amphibians, although much of the nomenclature is now superseded. Work prior to Taylor's series by Boulenger, Cope, Dunn and Peters is either outdated or summarised in Savage (2002).

Two recent books have added to the extensive work by Savage (2002) and provide specialist, regionally specific information. Solórzano (2005) treated the snakes of Costa Rica and described much of the key literature and ecology of each species with pointers for future research. Guyer & Donnelly (2005) updated their individual

contributions within McDade *et al.* (1994) and have compiled a comprehensive book specialising on the herpetofauna of La Selva Biological Station and lowland forests of Costa Rica's Caribbean slope.

The most current species inventory for Costa Rica (Savage 2002) lists 173 classified species of amphibian native to Costa Rica (+ 1 introduced species; *Eleutherodactylus johnstonei*) and 217 species of native reptile of which 133 are snakes (+ 4 introduced species; *Hemidactylus frenatus*, *Hemidactylus garnotii*, *Lepidodactylus lugubris* and *Ctenonnotus cristatellus*). The number of new species of reptile and amphibian found annually has reached a climax for Costa Rica, although occasional discoveries and further revisions continue (Lips 1996; Lips & Savage 1996b; Savage 1997).

A variety of general herpetology texts cover essential background on the known biology, ecology, classification and conservation of herpetofauna with many tropical examples (Stebbins & Cohen 1995; Pough *et al.* 1998; Zug *et al.* 2001). More nationally specialist texts on Caribbean and Latin American species describe the evolutionary similarities and biogeography of herpetofauna across the neotropics (Crother 1999; Duellman 1990; Savage 2002).

1.12 Caño Palma's Herpetofauna

The herpetofauna of Caño Palma was first documented by Burger (2001) after several unpublished lists compiled since 1993. Burger's (2001) species list comprised 39 amphibians known from the Tortuguero region of which 22 species had been verified as seen in Caño Palma Biological Station forest and grounds.

After further species discoveries during this study the list of known herpetofauna for Caño Palma Biological Station forest and grounds was revised incorporating new knowledge on the taxonomy and distribution (Appendix 9.0). The revised species list for Tortuguero comprises 37 amphibians of which 26 amphibians have been verified as seen in Caño Palma Biological Station's forest and grounds (Table 1.12.1).

Table 1.12.1 Caño Palma Biological Station amphibia list 2009.

		LOCATION & NO. OF SPECIES FOUND:	
SCIENTIFIC NAME Note: () indicates a synonym	COMMON NAME Note: { } indicates the Spanish name	CAÑO PALMA	TORTUGUERO AREA
Class- AMPHIBIA	AMPHIBIANS	26	37
Order- Gymnophiona	Caecilians	1	1
Family- Caeciliidae	Caecilians	1	1
<i>Gymnopsis multiplicata</i>	Purple Caecilian	•	•
Order- Anura	Frogs & Toads	25	36
Family- Bufonidae	Toads	2	4
<i>Bufo coniferus</i> (<i>Incilius</i> clade)	Green Climbing Toad	•	•
<i>Bufo haematiticus</i> (<i>Rhaebo</i> clade)	Smooth Skinned, or Leaf-litter Toad		•
<i>Bufo melanochlorus</i> (<i>Incilius</i> clade)	Wet forest or Foothill stream Toad		•
<i>Bufo</i> (<i>Chaunus</i>) <i>marinus</i> (<i>Rhinella</i> clade)	Cane, Marine or Giant Toad	•	•
Family- Centrolenidae	Glass Frogs	1	3
<i>Centrolene ilex</i>	Ghost Glass Frog, Limon Giant Glass Frog	•	•
<i>Centrolene prosoblepon</i>	Emerald Glass Frog		•
<i>Hyalinobatrachium fleischmanni</i>	Fleischmann's Glass Frog		•
Family- Craugastoridae	Neotropical Leaf-litter Frogs	6	7
<i>Craugastor fitzingeri</i>	Common Rain, Barking, or Fitzinger's Robber Frog	•	•
<i>Craugastor mimus</i>	None assigned	•	•
<i>Craugastor noblei</i>	Noble's Leaf-litter, Rain, or Robber Frog	•	•
<i>Craugastor persimilis</i>	None assigned	•	•
<i>Craugastor polyptychus</i>	None assigned	•	•
<i>Craugastor ranoides</i>	Rain Frog		•
<i>Craugastor rugulosus</i>	Rugulose Rainfrog	•	•
Family- Dendrobatidae	Poison-dart Frogs	1	2
<i>Dendrobates</i> (<i>Oophaga</i>) <i>pumilio</i>	Strawberry Poison-dart Frog, Blue-Jeans Frog	•	•
<i>Phyllobates lugubris</i>	Striped Poison Dart-frog, or Lovely Dart Frog		•
Family- Eleutherodactylidae	Neotropical Frogs	1	1
<i>Diasporus</i> (<i>Pristimantis</i> / <i>Eleutherodactylus</i>) <i>diastema</i>	Dink Frog, Common Tink Frog	•	•
Family- Hylidae	New World Treefrogs	11	12
<i>Agalychnis callidryas</i>	Red-eyed Leaf Frog, Red-eyed Treefrog	•	•
<i>Cruziohyla</i> (<i>Agalychnis</i>) <i>calcarifer</i>	Splendid Leaf Frog, Barred Treefrog		•
<i>Dendropsophus</i> (<i>Hyla</i>) <i>ebraccatus</i>	Painted, Hourglass, Clown, or Harlequin Treefrog	•	•
<i>Dendropsophus</i> (<i>Hyla</i>) <i>phlebodes</i>	Yellow Treefrog	•	•
<i>Hyloscirtus</i> (<i>Hyla</i>) <i>palmeri</i>	Palmer's Treefrog	•	•
<i>Hypsiboas</i> (<i>Hyla</i>) <i>rufitelus</i>	Red-Webbed Treefrog	•	•
<i>Scinax boulengeri</i>	Boulengeri's Treefrog	•	•

<i>Scinax elaeochroa</i>	Olive Treefrog	•	•
<i>Smilisca baudinii</i>	Mexican, Baudin's, or Van Vliet's Treefrog	•	•
<i>Smilisca phaeota</i>	Masked Treefrog	•	•
<i>Smilisca sordida</i>	Drab Treefrog	•	•
<i>Tlalocohyla (Hyla) loquax</i>	Red-Legged Treefrog	•	•
Family- Leptodactylidae	Neotropical Frogs	2	2
<i>Leptodactylus melanonotus</i>	Sabinal or Black-Backed Frog	•	•
<i>Leptodactylus pentadactylus</i>	Smokey Jungle Frog, Central American Bullfrog	•	•
Family- Microhylidae	Microhylid frogs	0	1
<i>Gastrophryne pictiventris</i>	Southern Narrow-mouthed Toad		•
Family- Ranidae	Holarctic & Paleotropic Frogs	1	2
<i>Rana vaillanti</i>	Vaillant's Frog, Tropical Bullfrog	•	•
<i>Rana warszewitschii</i>	None assigned		•
Family- Strabomantidae	Neotropical Frogs	0	1
<i>Pristimantis (Eleutherodactylus) ridens</i>	Pygmy Rain Frog		•
TOTAL SPECIES:		26	37

1.13 An Introduction to the Amphibian Species Studied

The following information details amphibian species that were investigated in this study. The information summarises the current ecology known for each species. Some species present at Caño Palma Biological Station were deemed unsuitable for the survey techniques used herein. This was because they were infrequently encountered (i.e. those species recorded only once since 1993), significantly out of range (i.e. those species that exist in high canopy greater than 3.0 m) or especially rare (i.e. those species deemed critically endangered).

Savage (2002) provides further information for the remaining species at Caño Palma that do not form part of this study. In total 16 species representing 5 families were included in this study. Eight species were terrestrial and 8 were arboreal or climbing species. All species were anuran amphibians. Table (1.13.1 pg. 60) provides summaries of the life history for each study species.

The classification of several of the specimens in this study changed during its completion. Faivovich *et al.* (2005) readdressed the systematic order of the family Hylidae and Frost *et al.* (2006) recently readdressed the whole of the Subclass

Lissamphibia. Vidal & Hedges (2005), Hedges *et al.* (2008) and Kelly *et al.* (2009) provide further revisions at family level that affect the cladistic nomenclature of tropical herpetofauna. While many herpetologists have adopted these new taxonomies entirely, this study adhered to recommendations within Frost *et al.* (2006) and Smith & Chizar (2006).

Frost *et al.* (2006) and Smith & Chizar (2006) recommended that traditional names be used together with former nomenclature on a temporary basis for several years following the taxonomic shuffle to maintain integrity and awareness of the name changes through literature. This was achieved by a system of introducing each new species with the formerly acknowledged genus first and the newly identified subgenus second. For example, although the changes proposed by Frost *et al.* (2006) for the genera *Bufo* and *Rana* were made at the generic level, biologists who wish to recognize the subdivisions of these genera, but maintain the stability of familiar species names and still follow the rules of the International Code of Zoological Nomenclature (ICZN), may choose to recognize newly created subdivisions of these genera as subgenera (Smith & Chizar 2006; Hillis 2007). Under ICZN rules, the subgenus category may follow the genus name in parentheses, e.g., *Bufo (Chaunus) marinus* or *Rana (Lithobates) pipiens*.

This cross linking of the genera in nomenclature was recommended because the majority of the new names proposed by Frost *et al.* (2006) are disconnected from the old genera in previous amphibian literature. For example; the literature dealing with frogs of the *Bufo* and *Rana* genera in the northern hemisphere is enormous. Adopting this new taxonomy will help future researchers to identify the genera included in this study and find it among literature.

There is no requirement in the ICZN taxonomic recommendations that demands changes such as those of Frost *et al.* (2006) are mandatorily followed. When the hypotheses of relationships in Frost *et al.* (2006) have been tested with additional data, sufficient taxon sampling, further analytical methods, and a trend in use, the changes will likely become permanent (Hillis 2007).

Table 1.13.1 Species studied; breeding strategy, diel habits, habitat; Noc = nocturnal, Dir = diurnal, DF = deep forest, E = edge, TP = temporary pools, PP = permanent pools, LL = leaf-litter, A = arboreal, T = terrestrial, (T) = arboreal but also terrestrial.

Species	Family	Activity	Habitat	Arboreal / Terrestrial	Reproductive Strategy	
<i>Bufo coniferus</i>	Bufonidae (2)	Noc	DF/E/TP/PP/LL	A (T)	Aquatic	Tadpole
<i>Chaunus marinus</i>		Noc	E/TP/PP/LL	T	Aquatic	Tadpole
<i>Craugastor polyptychus</i>	Craugastoridae (4)	Dir/Noc	DF/E/LL	T	Terrestrial	Direct Development
<i>Craugastor fitzingeri</i>		Dir/Noc	DF/E/LL	T	Terrestrial	Direct Development
<i>Craugastor noblei</i>		Noc	DF/LL	T	Terrestrial	Direct Development
<i>Craugastor persimilis</i>		Dir/Noc	DF/E/LL	T	Terrestrial	Direct Development
<i>Oophaga pumilio</i>	Dendrobatidae (1)	Dir	DF/E/LL	A (T)	Terrestrial	Tadpole
<i>Agalychnis callidryas</i>	Hylidae (5)	Noc	DF/E/TP/PP	A	Aquatic	Tadpole
<i>Dendropsophus phlebodes</i>		Noc	DF/TP/PP	A	Aquatic	Tadpole
<i>Hypsiboas rufitelus</i>		Noc	E/TP/PP	A	Aquatic	Tadpole
<i>Scinax elaeochrous</i>		Noc	E/TP/PP	A	Aquatic	Tadpole
<i>Smilisca baudinii</i>		Noc	E/TP/PP	A	Aquatic	Tadpole
<i>Leptodactylus melanonotus</i>	Leptodactylidae (2)	Noc	DF/TP/PP/LL	T	Aquatic	Tadpole
<i>Leptodactylus pentadactylus</i>		Noc	DF/E/PPLL	T	Aquatic	Tadpole
<i>Rana vaillanti</i>	Ranidae (1)	Noc	E/TP/PP/LL	T	Aquatic	Tadpole
<i>Pristimantis diastema</i>	Strabomantidae (1)	Noc	DF/E/LL	A	Terrestrial	Direct Development

1.13.1 Bufonidae

1.13.1.1 *Bufo coniferus* (Cope); (Plate 1.13.1.1a/b)

This small toad species (53-72mm males/76-94mm females; snout vent length [SVL]) has angular parotid glands, webbing between the toes and a distinct enlarged series of lateral warts that are tipped with elongate spines. It is olive green to dull grey or brown with contrasting dark and light blotches. The venter is a dirty white colour and the eye has a green to brown iris (Savage 2002).

The species is common in lowland tropical wet, moist and premontane forest. It is a nocturnal, scansorial toad often found several metres above ground in foliage and small tree branches. It is not yet known why this toad climbs although such behaviour may be in relation to its diet, which comprises almost exclusively ants (Toft 1981).

Bufo coniferus calls from, and breeds in, temporary and permanent shallow pools. The call is a noisy deep trill and can be heard throughout the day (Savage 2002). *B. coniferus* breeds during heavy rains and can be found in amplexus during the wet season. At Caño Palma, *B. coniferus* was an infrequent visitor to the ground's pond, but is found regularly in the *Manicaria* areas of Caño Palma's forest close to temporary pools and permanent swamps. Juveniles can also be found at Caño Palma. They are virtual replicas of the adults, approximately 14mm SVL and usually brighter in colour (Plate 1.13.1.1a).

1.13.1.2 *Bufo (Chaunus) marinus* (Linnaeus); (Plate 1.13.1.2)

Chaunus marinus is Costa Rica's largest amphibian (85-145mm males/90-175mm females SVL; also to 238mm SVL in South America). *C. marinus* dorsum is various shades of brown or grey with mottled irregular, brown blotches or spots and a cream, dusky mottled venter. Juveniles have transverse cross bars on the upper surfaces. Adult males tend to be a more uniform cinnamon colour. The most notable field features of this species are its highly prominent cranial crest and large parotid glands. *C. marinus* is found in all lowland and premontane zones, especially in disturbed habitats, secondary forests and around human habitation (Savage 2002).

Plate 1.13.1.1a Juvenile *Bufo coniferus* (© Twan Leenders 2007

www.amphibiaweb.com).

Plate 1.13.1.1b An adult *Bufo coniferus* on *Manicaria saccifera* leaf; Caño Palma
(Liam Fahey 2008).

This species eats a diverse array of prey including molluscs, worms, arthropods, large coleopterans, lizards, frogs, small snakes and even juvenile *Chaunus marinus* (Strüssmann *et al.* 1984). It is one of the most studied amphibians in the world because of its conspicuous nature and success in colonising non-native countries as a ‘weed’ species (Lever 2001; Urban *et al.* 2007).

Plate 1.13.1.2 An adult male *Chaunus marinus* calling from a hammock at the Biological Station pond (Paul Grant 2002).

In some countries it has caused negative effects on local predators and native species, whereas in others it has provided a beneficial role in ecological communities (Williamson 1999; Crossland 2000; Phillips & Shine 2005). Easteal (1986) reviews the extensive literature on the species. Much of the known ecology of *Chaunus marinus* in its natural environment of Central and South America was documented by Zug & Zug (1979). This nocturnal species is a prolific coloniser of secondary areas and can reach huge densities of up to 300/ha in agricultural settings, although it is more typically found at 25-30/ha in natural forest zones (Zug & Zug 1979). It is highly mobile, with a home range of 160m² and remains active in moist conditions throughout the year.

Breeding occurs opportunistically and usually during the onset of the wet season. Males call from the edge of permanent water bodies. The edges of rivers and streams are also used for breeding although swamps, pools, ponds and ditches are favoured.

The eggs are laid in paired strings of 2500-25000 (each egg is 1.7-2.0mm in length) and are as noxious with Bufotoxin as tadpole and adults. Eggs hatch in 36 hrs to 4 days and can produce thousands of tadpoles. The tadpoles are highly sociable and metamorphose in 30-80 days depending on temperature. The tadpoles are highly resistant to desiccation, being able to survive out of water for 10 hours (Valerio 1971). *Chaunus marinus* juveniles grow extremely fast and reach sexual maturity in just one year (Zug & Zug 1979). Juveniles and sometimes adults are preyed upon by a few select species of fish, crocodilians, birds, snakes, turtles and mammals that are able to tolerate Bufotoxin. At Caño Palma, *C. marinus* is a resident species found in the Biological Station pond and is only rarely encountered in Caño Palma's forest.

1.13.2 Craugastoridae

1.13.2.1 *Craugastor (Eleutherodactylus) fitzingeri* (Schmidt); (Plate 1.13.2.1)

The family Craugastoridae was, until recently, part of the Leptodactylidae which comprised the largest known vertebrate family, with over 700 species (Wells 2007; Hedges *et al.* 2008). The genera *Craugastor* and *Eleutherodactylus* (previously grouped as *Eleutherodactylus*) comprise the largest number of frogs per genus in Latin America. Many species are polymorphic and polychromatic making taxonomic descriptions and life history difficult to elucidate (Janzen 1983; Leenders 2001; Savage 2002; Guyer & Donnelly 2005). Some species are so infrequently seen that nothing is really known of them, whereas others are so abundant their life history is among the most documented of tropical frogs (Savage 2002). The Leptodactylidae and Craugastoridae are a vital part of the forest floor ecosystem and form one of the largest fractions of invertebrate predators. They are themselves also a large prey resource (Savage 2002).

Craugastor fitzingeri is a moderate sized frog (23-35mm males/36-53mm females SVL) and is distinguished within its genus by possessing gracile legs with light spots on the posterior thigh surface. It also has a sharply pointed snout, large tympanum and white mid-gular stripe that is present in both adults and juvenile. Its dorsum has highly variable markings in shades of gold to bronze and numerous small pale yellow spots. Sometimes its dorsum has a cream to orange mid-dorsal stripe that is bordered by a thin black line.

Craugastor fitzingeri is widely distributed in Central America from eastern Nicaragua across both Atlantic and Pacific versants of Costa Rica and through most of Panama. It is also found in the western lowlands of Colombia. It is ubiquitous in Costa Rica and is abundant in lowland wet forests. In tropical dry forest it is restricted to riparian areas. *C. fitzingeri* is active both day and night and prefers shrub and edge layer habitat but can also found in deep forest (Lynch & Myers 1983). At Caño Palma it is a frequently encountered frog. At night, both sexes are encountered in understorey vegetation 0.5-1.6m, usually just above ground. During the day they are concealed in leaf-litter on the forest floor (Miyamoto 1982; Höbel 1999). Males call from stumps and leaf-litter at dusk and dawn, especially after heavy rains although they rarely call through an entire night (Lieberman 1986). The calls vary geographically and although primarily act to attract females, seem to assist males to locate each other (Höbel 2005). Calling frequencies are lower at dusk and assist in avoiding predation by specialist frog eating bats (Tuttle & Ryan 1981; Lynch & Myers 1983; Höbel 2005). The call is also tediously difficult to trace, which possibly assists in reducing vulnerability to predation. Eggs are laid in leaf-litter and tree buttresses (Ryan 2005). Egg clutches for this species range from 24-92 and are attended by females (Lynch & Myers 1983; Savage 2002). Hatchlings are 7-11mm SVL and juveniles 14-15mm SVL (Ryan 2005).

1.13.2.2 *Craugastor (Eleutherodactylus) noblei* (Barbour & Dunn); (Plate 1.13.2.2)

This masked grey-brown leaf-litter frog has a long protruding snout, bright yellow venter and a distinct longitudinal glandular ridge. Its dark mask extends beyond the shoulders into the lateral region.

Plate 1.13.2.1 Adult *Craugastor fitzingeri* (© Paddy Ryan).

Plate 1.13.2.2 Juvenile *Craugastor noblei* (© Andrew J. Crawford 2002).

It has large golden eyes with a horizontal elliptical pupil. A dark brown hourglass spot is usually present on the back. This frog lacks the usual vocal sac necessary to make a call but this does not mean they are incapable of making sound. The ecology of *Craugastor noblei* is poorly known and reproduction and parental care has only recently been discovered (Savage 2002; Whitfield & Pierce 2003). At Caño Palma this species is rare and only ever encountered in the leaf-litter during quadrat samples. The exact call for this species is still yet to be determined.

1.13.2.3 *Craugastor (Eleutherodactylus) polyptychus* (Cope);
(Plate 1.13.2.3 a/b)

This very small (13-23mm males/13-26mm females SVL), common, leaf-litter frog has projecting tubercles on the hands and feet. The dorsum and lateral region is granular, warty and brown in colour. Some specimens exhibit a mid dorsal stripe, heavier wart distribution on the body and highly polymorphic colours and markings. The groin and hind limbs are more consistent in their colour and are usually covered in a reddish suffusion. Males have no nuptial pads.

Craugastor polyptychus, and its syntopic montane parent species *Craugastor bransfordii*, both exist in lowland moist, premontane and wet forests. Together they are without question two of the most abundant species in the lowland tropics of Costa Rica (Lieberman 1986; Guyer & Donnelly 2005). Population densities are often high and have been recorded at 1200/ha during the late dry season (Lieberman 1986).

The frogs actively forage in the daytime eating a wide variety of prey including beetles, mites, spiders and isopods in huge numbers. They exhibit a strong ontogenetic shift in the size of their prey items, which in turn affects the number and type of prey consumed at different times of the year (Whitfield 2005). The species choice of prey is linked to its seasonal availability which can also act as a driver, forcing seasonal breeding (Watling & Donnelly 2002; Whitfield 2005). Breeding takes place opportunistically and some females oviposit several times a year. Males call sporadically from under leaves on the ground and mating appears to take place within leaf-litter at night (Scott 1983).

Plate 1.13.2.3a An adult *Craugastor polyptychus* on leaf-litter in deep forest
(© Maciej Pabijan 2007).

Plate 1.13.2.3b An adult *Craugastor polyptychus* on leaf-litter
(© Maciej Pabijan 2007).

Due to its polymorphic nature, *Craugastor polyptychus* taxonomy has been subject to revision over the years (Miyamoto 1983; Savage & Villa 1986; Savage 2002; Crawford 2003). Recent phylogenetical analyses have demonstrated that this species has high nucleotide diversity within populations, large divergence between populations and high species diversity. Geologically young and dynamic regions in the neotropics can support very old lineages of this species and harbour great levels of genetic diversity within populations (Crawford 2003).

1.13.2.4 *Craugastor (Eleutherodactylus) persimilis* (Barbour)

This common, very small, brown frog is almost indistinguishable from *Craugastor polyptychus* in colour, pattern and size. It also resembles *C. polyptychus* in its ecology and biology and was only recently distinguished taxonomically from *C. polyptychus* (Savage 2002). It has prominent tubercles under the fingers and toes. Finger II is also longer than finger I in this species (see Duellman & Trueb [1986] for palm diagrams). Adult males have no nuptial pads. The above diagnostic features, distinguish *Craugastor persimilis* from other *Craugastor* species at Caño Palma. *C. persimilis* has a large whitish inguinal gland, and like *C. polyptychus*, the groin and hind limbs are covered by a reddish suffusion. The occurrence of this species at Caño Palma was verified by Federico Bolaños at the University of Costa Rica. Field identification was tested alongside laboratory identification although in the field some juveniles of *C. polyptychus* and *C. persimilis* were almost indistinguishable.

1.13.3 Dendrobatidae

1.13.3.1 *Dendrobates (Oophaga) pumilio* (Schmidt); (Plate 1.13.3.1 a/b)

The following information is documented from research that took place predominantly at La Selva Biological Station (McDade *et al.* 1994) as well as from works by Limerick (1980), Weygoldt (1980), McVey *et al.* (1981), Lieberman (1986), Donnelly (1989a; 1989b; 1991), Brust (1993), Pröhl (1997; 2003) and Savage (2002). This small (adults 17.5-24.0mm SVL), robust, phytotelmic species is one of the most studied tropical amphibians (Savage 2002; Lehtinen 2004; Lötters *et al.* 2007).

It has blue legs, a bright red body and a smooth dorsum. Its hands and arms are small and are often shades of blue to black. *Oophaga pumilio* is found in undisturbed forest and abandoned clearings of lowland wet and dry forest, mostly on the Atlantic versant of Costa Rica. It can be found in all habitat zones at Caño Palma.

Oophaga pumilio is active diurnally throughout the year, but is occasionally seen at night. It is often encountered in shaded forest moving through leaf-litter, on logs, buttresses and tree stems at a height below 2.0m (Han *et al.* 2007). Activity patterns for this species peak in the early morning and decline through the rest of the day (Graves 1999).

Oophaga pumilio prey comprises mostly of ants, mites and millipedes that are smaller than 3.0mm (Donnelly 1991). Dietary studies have shown that the species has a moderate degree of ontogenetic influence in its choice of prey size (Donnelly 1991). *O. pumilio*, like other Dendrobatid species, is characterized by an ability to sequester alkaloid-based chemicals throughout its body from its arthropod diet (Daly *et al.* 1995). The alkaloid composition of *O. pumilio* has been studied for over 30 years and has resulted in the detection of 230 alkaloids from 21 different structural classes (Daly & Myers 1967; Daly *et al.* 1987; Saporito *et al.* 2006). The alkaloids are predominantly histrionicotoxins, pumiliotoxins, de-cahydroquinolines and various izidine compounds that originate from dietary ants, millipedes and mites (Daly *et al.* 2005; Saporito *et al.* 2003; 2004; 2007). These chemicals afford the frog both intrinsic (e.g. snake predators) and extrinsic (e.g. mosquitoes) protection (Saporito *et al.* 2006; Weldon *et al.* 2006). The alkaloid profiles also differ considerably among populations of *O. pumilio* throughout its natural range (Daly *et al.* 1987; Saporito *et al.* 2006).

Population densities are high for this species, reaching 827/ha during the wet season. *Oophaga pumilio* has a home range of 2-16m² for males and 6-16m² for females (up to 38.5m² for females when not breeding). Sex ratios are even in primary forests yet strongly female biased in secondary forests with more abundant breeding resources (Pröhl 2002). Male *O. pumilio* defend general territories, nearby females and mating arenas (Pröhl 1997; Pröhl & Berke 2001; Pröhl 2003; Pröhl 2005). Male breeding territories typically range from 0.24-4.78m² and can be held for several years (Pröhl 1997; Pröhl & Hödl 1999).

Plate 1.13.3.1a Adult *Oophaga pumilio* (© Thomas Splettstöesser).

Plate 1.13.3.1b An adult *Oophaga pumilio* climbing a young understorey tree in Caño Palma Biological Station forest (Paul Grant 2002).

Males defend their breeding territory from logs and root buttresses that act as perches. Their call is a familiar and repetitive ‘chugg’. Calls vary subtly in their purpose and are used for advertisement to attract females, conduct courtship, or to defend against intruding males (Pröhl 2003). Calling usually occurs when a male is on a territory perch (Graves *et al.* 2005). Defensive calling is also positively affected by rainfall (Graves *et al.* 2005). Studies have shown that *Oophaga pumilio* will actively defend reproductive resources such as bromeliads, and the same is true for other tropical anuran species (Donnelly 1989a; Oliveira & Navas 2004). However, they do not always defend habitat specifically. Habitat resources required for breeding purposes have been shown to spatially govern female distribution which in turn influences male distribution (Pröhl & Berke 2001; Pröhl 2005).

In *Oophaga pumilio* communities, resident territory holders of both sexes are attacked by both neighbours and vagrants with peak activity for attack and defence occurring in the morning between 06:00-09:00 (Gardner & Graves 2005; Graves *et al.* 2005). When an intruding male infiltrates a territory at close range, the individuals may wrestle physically for up to 20 minutes to conclude dominance. Females, non-calling males and juveniles are not attacked physically by males in territory defence mode. Breeding females are also territorial during pre-nuptial periods and this again is linked to the need for reproductive and habitat resource protection (Pröhl & Berke 2001; Haase & Pröhl 2002). Vocal and physical defence of territory is a strong characteristic of other Dendrobatid frogs (Duellman 1966; Crump 1972; Wells 1980; Roithmair 1992). However, despite its vibrant defensive behaviour *O. pumilio* is known to live in sympatry with its Pacific versant species *Oophaga granulifera* in some montane parts of Costa Rica (Myers *et al.* 1995).

Mating in *Oophaga pumilio* appears to be polygamous and opportunistic, and occurs throughout the year (Pröhl & Hödl 1999). Males can be polygynous throughout their territory. Females engage in pre-courtship activities with several males to assess their fitness and quality (Pröhl & Hödl 1999). Courtship initiates when a female approaches a male in his territory. She assesses her mate by call properties before deciding on an ideal partner (Pröhl 2003). Courtship may last 10-180 minutes with no amplexus; a vent to vent posture is used. Clutch sizes are 3-5 in the field but up to 20

in captivity (Weygoldt 1980). Parental care is exhibited by both males and females. The male and female moisten eggs daily by emptying their bladder over the clutch. Hatching occurs after approximately 7 days (Limerick 1980). Upon hatching the female transports 1-4 of the tadpoles on her back to separate water filled axils in bromeliads or other plants with a notable water collecting bract (Young 1979) (Plate 1.13.3.1c).

Plate 1.13.3.1c An *Oophaga pumilio* tadpole in a rain-filled *Guzmania* sp. bromeliad (Todd Lewis 2005).

The female then returns to the plant daily during the morning to lay unfertilised eggs for the tadpole to eat. This activity is stimulated by a complex ‘begging’ behaviour by the tadpole that entices her to lay eggs into the leaf axil. The mother feeds only her own young. Tadpole rearing mothers terminate courtship whilst they are tending to larvae but do engage in defensive interactions with intruders, including other females (Haase & Pröhl 2002). This style of parental brood care strongly increases the reproductive success for this species (Townsend *et al.* 1984).

Metamorphosis by larvae is achieved between 43-52 days and young are 10mm standard length (SL). They achieve sexual maturity in approximately 10 months at about 19mm SVL. There is little data on longevity. Donnelly (1983) concluded that the population at La Selva was mostly comprised of ‘long-lived’ adults. Zimmermann & Zimmermann (1994) gave longevity of 4 years for captive *O. pumilio*.

On the archipelago of Bocas del Toro, Panama, *Oophaga pumilio* exhibits extraordinary intraspecific differentiation considering its recent genetic divergence (Summers *et al.* 1997; 2003). Adults on different islands boast sharp differences in colour (reds, blues, greens, oranges, yellows and blacks) and markings (spots, blotches, speckling and nondescript patterns) (Myers & Daly 1983). Further work on these populations has discovered that visual mate choice is driven by partial colour recognition in the species suggesting that the frog may have colour vision (Summers *et al.* 1999; 2003). The genus (*Oophaga*) was only recently assigned from *Dendrobates* by Grant *et al.* (2006). Current threats to the conservation of this species include over-collection and habitat degradation (Solis *et al.* 2009).

1.13.4 Hylidae

1.13.4.1 *Agalychnis callidryas* (Cope); (Plate 1.13.4.1)

This widely distributed species has been extensively studied and information herein is described from Donnelly & Guyer (1994), Duellman (2001) and Savage (2002). Sometimes known as the ‘Gaudy Leaf-frog’, this aesthetically coloured nocturnal anuran is common in swamp areas of lowland moist and wet forest and can also be found in disturbed areas and mangrove. *Agalychnis callidryas* is easily recognized by its bright red eyes, green dorsum, orange feet, white belly and yellow bars running through a blue lateral region. It is a slender, moderate sized tree-frog (30-59mm males/51-71mm females [SVL]). Only one other species is similarly coloured in the Tortuguero region; the rare and highly endangered *Agalychnis saltator*.

In the dry season *Agalychnis callidryas* spends much of its time avoiding desiccation, residing in palm fronds and high vegetation (Duellman 2001). During Caño Palma’s wet season this species is found abundantly in most temporary and permanent pools

where it gathers for breeding. Breeding occurs throughout the wet season (November to February) with peaks in June and October. Courtship occurs before, during and after nights with heavy rain. Males gather in vegetation close to pools, call and descend to the pool edge later in the night. *A. callidryas* has a characteristic ‘cluck’ call that can be heard easily among night-time tropical forest activity. The females follow the call, select a mate and climb into the pool to absorb water for egg mucous production. The female then carries the amplexant male to a deposition site.

Plate 1.13.4.1 An adult *Agalychnis callidryas* perched on a *Costus* sp. floret (Paul Grant & Todd Lewis 2002).

Clutches of 11-104 eggs are laid on the upper or underside of leaves overhanging the pool. Hatching of eggs is non-synchronous and occurs in 5-8 days. After a minimum development stage (usually a few days), eggs can hatch upon physical stimulus (e.g. rainfall, or strong wind), thus allowing hatching to commence upon suitable rainfall. Egg survival is around 63% due to heavy predation and tadpole hatches that do not fall directly into the pond. Metamorphs are 18-19mm SVL. *Agalychnis callidryas* is syntopic with nearly all other pond breeding Hylid species found in the lowland tropics of Costa Rica (Donnelly & Guyer 1994).

1.13.4.2 *Dendropsophus phlebodes* (Stejneger); (Plate 1.13.4.2)

This small (19-24mm males/23-28mm females SVL), nocturnal tree-frog has a tan brown-yellow dorsum with an irregular reticulum and dark lines. It has yellow thighs with faint brown bars on the tibia and axillary membranes. It is distinguishable from its virtually identical Pacific counterpart, *Dendropsophus microcephalus*, by the absence of a thin black dorsal line from snout to vent. *Dendropsophus phlebodes* turns a light grey colour during the day.

Plate 1.13.4.2 An adult *Dendropsophus phlebodes* resting on understorey leaf in daytime (Paul Grant & Todd Lewis 2002).

Dendropsophus phlebodes is a widely distributed species and moderately common in lowland wet, moist and premontane forest (Savage 2002). It occurs infrequently at Caño Palma. Reproduction can take place at any time of the year after heavy rain and mostly during the wet season with aggregations of adults occurring in shallow, grass filled seasonal pools (Donnelly & Guyer 1994; Duellman 2001). Adults are usually found on grasses and reeds at a perch height of between 1-2m.

Dendropsophus phlebodes is an occasional visitor to the Biological Station pond and can also be found in mixed vegetation sections of Caño Palma's forest, close to temporary pools and permanent swamps. Population data on *D. phlebodes* is limited to a few reports, despite their fairly frequent occurrence in lowland Atlantic forests (Savage 2002). It is known that males of the species are spatially organised at breeding pools by their call and therefore limit the carrying capacity of breeding adults per pool by calling isolation (Fouquette 1960).

1.13.4.3 *Hypsiboas rufitelus* (Forquette); (Plate 1.13.4.3)

This moderate sized (39-49mm males, 46-55mm females SVL) tree-frog has two morphs, one green with dark dorsal dots and a blotchy lichen coloured morph. At Caño Palma only the green morph was observed. Adults have a bright green dorsum (similar to a frog of the Centronelidae), white belly, blue groin, pale blue throat and bright red toe-webbing. Juveniles of the green morph do not have red toe-webbing and sometimes no groin and throat colour. Some juveniles have parallel red and white dorsolateral stripes. Both adult and juvenile have a few white specks on the venter and a thin white stripe from the fourth toe to the heel.

Hypsiboas rufitelus frequents lowland moist and wet forests where it is seldom seen outside of the reproductive period. This species favours edge pool habitat at Caño Palma although it occurs randomly around the Biological Station grounds and alongside the Caño Palma. The tadpole for this species has only recently been described and has previously remained undetected or possibly confused with that of *Scinax elaeochrous* (Hoffman 2005).

1.13.4.4 *Scinax elaeochrous* (Cope); (Plate 1.13.4.4)

This moderate sized tree-frog (26-38mm males/30-40mm females SVL) has distinct green bones, a yellow groin with translucent venter, blue-grey throat and a smooth green dorsum. This species has a notable protruding snout. It lacks finger webs and dorsolateral stripes (Savage 2002). This nocturnal species is found throughout lowland forests at elevations <800m (Duellman 2001). It is sometimes found in buildings and especially around garden ponds.

Plate 1.13.4.3 A green morph adult *Hypsiboas rufitelus* (© Brian Kubicki 2006
www.amphibiaweb.com).

Plate 1.13.4.4 Adult *Scinax elaeochrous* (© Brian Kubicki 2006
www.amphibiaweb.com).

At Caño Palma *Scinax elaeochrous* is an occasional visitor to the Biological Station pond and was also found in the *Manicaria* zones in Caño Palma's forest on the edge of temporary pools and permanent swamps. *S. elaeochrous* is the most frequently encountered Hylid frog at Caño Palma.

This species is a highly explosive breeder and rapidly congregates in hundreds around ponds during the first heavy rains of a wet season (Donnelly & Guyer 1994). Male *Scinax elaeochrous* call (a distinctive and dominant 'waaak') from dense vegetation around pools and amplexus takes place among aquatic vegetation in choked pools.

Eggs are laid in a mass near aquatic vegetation and hatch in 1-6 days (Savage 2002). The eggs are small (1.8mm diameter), black and white coloured, and embryos orient themselves vertically in the water. Tadpoles observed in swamps at Caño Palma had a white venter, stripes on the tail and a band through the eye. Metamorphs are 19-22mm SVL (Savage 2002). Juveniles are rarely seen and sexual maturity is reached in 1 year.

1.13.4.5 *Smilisca baudinii* (Dumeril and Bibron); (Plate 1.13.4.5)

Smilisca species differ from other Hylids by having a central skin structure on the throat that gives the appearance of a dual throat sack. *Smilisca baudinii* is a moderate to large sized (47-75mm males/56-90mm females SVL) brown tree-frog with variable dark dorsal blotches that are sometimes outlined by a thin green line. The under surfaces are creamy white and the head has a dark eye-mask stripe with barred lips. This species has a prominent series of humeral warts. Metachrosis is extreme in *S. baudinii* and its colours are highly variable patterns of grey, brown, yellow, green and tan.

Smilisca baudinii occurs in xeric, sub-humid and wet forest. It is common in lowland wet and dry forests and is a good coloniser of secondary forests, frequenting temporary ponds and flooded fields (Savage 2002). This species is an explosive, opportunistic breeder that usually commences breeding during the first rains of the wet season. *S. baudinii* breeds in virtually any body of water although it is most frequently found in ponds with multi-species assemblages of frogs (Duellman 2001;

Savage 2002). Males gather in hundreds to attract females and drown out other calling frogs with their booming 'whack' call. Eggs for this species are a black and cream colour (3.0mm diameter) and are laid within submerged pond vegetation. At Caño Palma *S. baudinii* is found in mixed forest and near swamp and pool habitat. It is frequently encountered near permanent pools in the north and western areas of the forest.

Plate 1.13.4.5 A typically coloured adult *Smilisca baudinii* on *Heliconia* sp. leaf (Paul Grant 2002).

1.13.5 Leptodactylidae

1.13.5.1 *Leptodactylus melanonotus* (Hallowell); (Plate 1.13.5.1)

This moderate sized (30-45mm males/35-55mm females SVL), robust species, lacks dorsolateral folds giving its body a cylindrical appearance. It has well developed toe fringes and black tipped tubercles on the lower surface of the tarsus. It is a uniform brown colour with a creamy white mottled underside and a mottled posterior thigh. *Leptodactylus melanonotus* is a common nocturnal species in its range and is active

all year round. It can be found in temporary ponds, ditches, swamp margins and pastures in the lowland and premontane wet forests (Gregory 1982; Savage 2002). Both sexes congregate at the margins of streams and shallow water bodies. Its diet comprises a variety of small leaf-litter arthropods although this species has also been known to scavenge dead items of prey that also include dead tadpoles (Lewis *et al.* 2008). Males call from underneath mats of vegetation, among roots, in grass tussocks and are extremely shy. Resident males are territorial and display by press-up movements to other infiltrating males. If an intruder comes close then a tussle ensues with biting until one frog retreats (Brattstrom & Yarnell 1968).

Breeding occurs opportunistically in the wet season and commences with the onset of heavy rains. Amplexus takes place in shallow waters. As the eggs are laid the male produces glandular secretions to encase the eggs in foam. The foam is very dense, frothy and floats on water. A nest may contain 1-2000 eggs of 1.0mm in diameter. Heavy rains wash advanced larvae out of the nests over days or weeks later. The foam that is secreted by *Leptodactylus melanonotus* can also resist desiccation if the eggs are laid in an ephemeral pool. This allows some survival chance if further onset of rain is possible. It is not known if the tadpoles exhibit phenotypic plasticity. Small juveniles are approximately 16.0mm SVL (Savage 2002).

1.13.5.2 *Leptodactylus pentadactylus* (Laurenti); (Plate 1.13.5.2)

This large (169mm males, 181mm females SVL), ground dwelling anuran has a brown wood-grain dorsal pattern, striking black and white markings around the lip area, posterior bars on limbs, linear skin folds and red flash colouration on the thighs. Males have a keratinized spine next to the thumb and two smaller spines on the belly.

Leptodactylus pentadactylus has a voracious appetite and highly variable diet, feeding on virtually any prey sizeable enough to be swallowed. Prey items include small mammals, bird chicks, snakes and other frogs - including toxic *Dendrobates* and *Oophaga* sp. It is also the only New World frog known to eat scorpions (Lourenco & Cuellar 1995). Its hardy tadpoles can survive on a carnivorous or herbivorous diet and in one study were able to resist desiccation for 156 hours (6.5 days) (Valerio 1971).

Plate 1.13.5.1 An adult *Leptodactylus melanonotus* in a pool
(© William Leonard 2005 www.amphibiaweb.com).

Plate 1.13.5.2 An adult *Leptodactylus pentadactylus* on *Heliconia* sp. leaf; note the striking black and white lip markings (Paul Grant & Todd Lewis 2002).

Leptodactylus pentadactylus can be located by its distinctive eye-shine that is as noticeable as that of a Caiman (*Caiman crocodilus*). Interestingly, it can also produce a loud screaming distress call when caught, which is similar to that of a young Caiman in distress (LeVering 1999; Bernal 2006). This yelp attracts brooding female Caiman. There is some speculation that this is an evolutionary behavioural adaptation, developed to assist this species to escape in times of predation by recruiting curious female Caiman toward the frog (Savage 2002).

1.13.6 Ranidae

1.13.6.1 *Rana vaillanti* (Brocchi); (Plate 1.13.6.1a/b)

The genus *Rana* is among the most studied on earth because of its wide distribution, habitat tolerance, recurrent phenology, documented breeding cycle and tenacity to breeding ponds and pools (Wilbur 1980; Duellman & Trueb 1986; Duellman 1999; Wells 2007). A wealth of literature and studies have been conducted on one European species (*Rana temporaria*) and several North American species (*Rana muscosa*, *Rana sevosia*, *Rana pretiosa*, *Rana sylvatica* and *Rana macrocnemis*) (Loman 1984; Berven 1990; Tarkhnishvili 1999; Beebee & Griffiths 2000; Pope & Matthews 2001; Richter *et al.* 2001; Richter & Seigel 2002; Watson *et al.* 2003; Vasconcelos & Calhoun 2004).

In comparison neotropical Ranids have received much less attention and literature comprises mostly of work on taxonomic revisions with only a handful of population and reproduction studies (Savage 2002). Costa Rica has 5 species of Ranid frog. One is a lowland species, two are solely montane species and the remaining two are widely distributed across ecotones in the country. *Rana vaillanti* is one of the widely distributed species in Costa Rica occurring in lentic waters within lowland dry, moist and wet forests. It is a medium sized Ranid (67-94mm males/76-125mm females SVL) with strong and long back legs. It has a brown dorsum that becomes green anteriorly. It has prominent dorsolateral folds, a cream underside, large golden eyes and a pointed snout. Mature females are often completely speckled brown and males are more often green with posterior brown bodies and hind legs.

Plate 1.13.6.1a Adult *Rana vaillanti*. Note the prominent dorsolateral skin folds connecting with the eye (Paul Grant & Todd Lewis 2002).

Plate 1.13.6.1b An adult *Rana vaillanti* in pool (© William Farrington).

Rana vaillanti is semi-aquatic and occurs in shallow pond, lake, river and floodplain margins. It is a dominant pool side species and can out-compete other frogs for calling perches by attracting large densities of conspecific males to breeding pools. However, it can tolerate a multi species assemblage pool (Ramirez *et al.* 1998). *R. vaillanti* is active nocturnally and occasionally diurnally. It is a generalist sit-and-wait predator that remains in close association with breeding habitat. A recent dietary analysis revealed that adults of the species prey on terrestrial, and sometimes, aquatic invertebrates with a high percentage of prey being Dipteran larvae and Decapod crustaceans (Ramírez-Bautista & Lemos-Espinal 2004). However, such a prey base composition is likely to exhibit localised preferences in taxon and may vary between sites as the frog is a generalist predator (Savage 2002).

Ramirez *et al.* (1998) studied a population of *Rana vaillanti* in Veracruz, Mexico. They recorded a consistent year round sex ratio of 41.5% male and 52.4% female (6.4% juvenile), indicating that reproduction occurs year round and opportunistically in permanent suitable habitats. Lee (2000) recorded egg-laying by a population of *R. vaillanti* in Belize in February, showing just how opportunistic the species is in its breeding strategy. Both studies found that there was a clear drive for reproduction and calling during the onset of the wet season.

1.13.7 Strabomantidae

1.13.7.1 *Pristimantis (Eleutherodactylus) diastema* (Cope); (Plate 1.13.7.1)

Pristimantis diastema is a tiny (16-21mm males/18-24mm females SVL), semi-arboreal frog that is highly variable in colour and markings. During the day its upper surfaces are usually dark grey to brown with longitudinal bars, stripes and spots. At night individuals can be almost uniform light pink to grey. This species lacks heel tubercles and an obvious groin pattern.

Pristimantis diastema is widely distributed across the whole of Costa Rica with the greatest densities in lowland moist and dry forest. Food comprises a wide variety of arthropods and especially ants (up to 95% of the diet at La Selva Biological Station [Savage 2002]). *P. diastema* is heard abundantly in the forest by its distinctive, loud

and very sharp ‘tink’ call. Calling continues all night with a peak from 22:00 to 02:00. This call is highly important for *P. diastema* as it can mediate the spatial distribution of males (Wilczynski & Brentowitz 1988). Wilczynski & Brentowitz (1988) found that spatial distribution was non-random and can be 5-50m apart.

Plate 1.13.7.1 An adult *Pristimantis diastema* on a leaf at night (© T. Beth Kinsey 2006).

Densities in leaf-litter during the daytime have been found to be 37/ha (Lieberman 1986) but this quote may underestimate the true numbers because many also hide above ground in the daytime. Locating this species is difficult due to its highly variable perch heights (1.5m-35m). Acoustic surveys are sometimes preferred for abundance data collection (Savage 2002).

Reproduction occurs throughout the wet season. Males approach females that enter their territory and call continuously. The male lifts his legs up and down and upon acceptance the female touches his vocal sac with her snout. The male then leads the female to the nesting site (usually a leaf petiole, bromeliad, or fissure in tree bark) to engage in amplexus. Females can exhibit agonistic behaviour to evict other individuals that invade a nest site (Savage 2002). Females lay 11-19 eggs that are 4.0-4.5mm diameter on the ground among leaf-litter (Ovaska & Rand 2001; Whitfield 2006). In some populations males as well as females exhibit parental care by attending the clutch to moisten them by relieving their bladder over the eggs (Savage 2002; Whitfield 2006). Hatching occurs direct from the egg after 23-26 days. Hatchlings are tiny and juveniles are classed as those sized <10.5mm SVL. At Caño Palma this species is ubiquitous across all habitat zones and can be heard calling at a variety of perch heights and from a range of shrubs, vegetation and substrate.

1.14 The Ecology of Herpetofauna in Floodplain Environments

Biological communities in aquatic ecosystems are complex and comprise hundreds of plant and animal species structured in response to physical, chemical, biotic and abiotic changes (Huggenberger *et al.* 1998; Brönmark & Hansson 2005; Naiman *et al.* 2005). The role of natural disturbance within aquatic ecosystems is linked to these abiotic and biotic interactions. It comprises various cyclic changes (seasonal solar radiation, temperature, discharge and leaf fall) and less predictable, but longer lasting events (e.g. major flooding, fires and extreme winds), which can affect the entire community structure (Pickett & White 1985; Townsend 1989; Yount & Niemi 1990; Wootton *et al.* 1996).

These natural disturbance cycles in aquatic ecosystems can have short and long term effects on herpetofauna that is not fully understood yet (Woolbright 1991; Henderson & Berg 2005; Hawley 2006). Aquatic organisms including amphibians have evolved a variety of strategies to cope with natural climatic disturbance that include; plasticity of age of metamorphosis, development of drought resistance, selection of water-bodies with long hydroperiod, and exploitation of different niche habitats (Wiggins *et al.* 1980; Woodward 1982; Duellman & Trueb 1986; Newman 1989; Dodd 1994; Blaustein *et al.* 1999; Hartel *et al.* 2006; Wells 2007).

Amphibians are governed in abundance and distribution by geography (Duellman 1999) and, due to their physiology, by stochastic environmental and spatial variables (Connell 1983; Duellman & Trueb 1986; McCarthy 1997; Parris 2004). Hydroperiod is an environmental variable shown to affect amphibians (Babbitt *et al.* 2003; Baber *et al.* 2004). In the tropics it can be a feature that indirectly manipulates the ecology of the species present in specific habitats (Zimmerman & Simberloff 1996; Watling & Donnelly 2002; Parris 2004; Mamede & Alho 2006). The ‘Riverine Barrier Hypothesis’ states that river environments and their hydroperiods can divide populations genetically, driving species diversity forward (Salo *et al.* 1986). This hypothesis is proven for a number of tropical animals and plants, and select widespread species of amphibian (Wynn & Heyer 2001). However, the notion does not hold true for all species. Some species of Leptodactylidae have shown less genetic divergence across rivers and may exhibit some migration between water barriers (Gascon *et al.* 1998). It is suggested that where amphibian assemblages occur in altered populations along riparian gradients they may be comprised of a nested subset of the larger species group found within the wider landscape (Gardner *et al.* 2007b).

Aquatic breeding amphibians, their ecology and adaptation to ephemeral ponds and pools has been studied in depth for a number of amphibians throughout herpetological history (Duellman & Trueb 1986; Stebbins & Cohen 1995). It has been suggested that periods of inundation in ponds and pools help form habitats and topographical gradients along which amphibian assemblages are organised (Morand & Joly 1995; Zampella & Bunnell 2000). However, there is little quantitative evidence to support this. Historically, most experimental work on inundation effects on amphibians has been of a biological nature, addressing issues of physiological tolerance by adults and larvae (Duellman & Trueb 1986; McDiarmid & Altig 1999). Experimental studies on tolerance to submersion by amphibians and biological aspects of integumentary oxygen absorption are documented (Duellman & Trueb 1986; Wells 2007). It is known that many amphibians combine breathing through a primitive lung or set of lungs with additional dermal oxygen intake through their moist, semi-permeable skin (Young 1991; Duellman and Trueb 1986; Wells 2007).

More specific physiological studies (especially relating to the desiccation of pool habitats) have linked hydroperiod fluctuation to plastic responses shown by

developing eggs and metamorphosing tadpoles (Loman 1988; Brady & Griffiths 2000; Loman 2002; Loman 2003; Wells 2007). Some of these studies reveal that tadpoles metamorphose into froglets faster when water evaporates. The tadpoles are also responsive to a combined effect of hydrological desiccation and tadpole density-dependency although some populations may not exhibit this response if they are isolated (Brady & Griffiths 2000). Presence of chemical cues from ammonia excretions by predators also assists in accelerating metamorphic development of amphibians living in pools with fluctuating water levels (Hecnar & M'Closkey 1997; Kiesecker *et al.* 1999; Kats & Ferrer 2003).

Studies on the affects of unpredictable or extreme hydroperiod cycles on amphibians in natural environments are few and amount mostly to random observations in riparian ecotones (Jakob *et al.* 2003; Richter *et al.* 2003). Studies on the functional ecology of herpetofauna in floodplain environments are equally lacking and those that do exist document larger arterial river systems with extensive overspill of floodplain areas (Morand & Joly 1995; Gascon *et al.* 1998). The majority of studies on inundation have focused on temperate climates as the following examples show;

- Degani & Kaplan (1999) studied 41 habitats containing 6 amphibian species in northern Israel and examined their environmental relations.
- Donnelly *et al.* (2001a; 2001b) studied the herpetofauna of the river Kissimmee in central Florida to investigate the affects of conversions in channel morphology on amphibians.
- Tarkhnishvili & Gokhelashvili (1999) studied the spatial structure and population dynamics of *Rana macrocnemis* in riparian and hammock pools in the river Nedzura, a tributary of the river MtKvari, Georgia, United States.
- Gubányi & Creemers (1994) studied distribution and population structure of *Rana* species in the Szigetköz floodplain of the river Danube, Hungary. In more recent studies of the same stretches of river, Kovács (2002) reported on amphibian species in oxbow lakes, gravel pits, fishponds, backwaters and Alder Carr swamps.
- Ogielska *et al.* (1998) reported the effect of irregular flooding of the river Odra, Poland, on the dispersal of amphibians in metapopulations.

- Richter & Seigel (2002) studied *Rana sevosa* in isolated areas in a coastal plain forest of southern Mississippi.
- In the Niger Delta Basin, southern Nigeria, Akani & Luisella (2002) report that amphibians are suffering from notable declines across all genera.
- Bosman *et al.* (1997) reported the affects of inundation of the river Rhine, Holland, in an experimental and natural setting for hibernating *Bufo bufo* and *Bufo calamita*.
- Jakob *et al.* (2003) explored breeding phenology and larval distribution in 183 Mediterranean temporary ponds over 3 years in the Roque-Haute nature reserve, southern France.
- Cogălniceanu *et al.* (2000) studied feeding and dietary preference of amphibians along the Romanian section of the Danube floodplain.
- Hirai (2004) studied diet composition of *Rana limnocharis* in ephemeral pools and sand bars in the floodplain habitats of the river Kizu, Japan.
- Teixeira *et al.* (2004) produced a similar study to Hirai (2004), in the Espirito Santo state in southeast Brazil, for the anuran *Pseudis bolbodactyla*. Both Hirai (2004) and Teixeira *et al.* (2004) describe the ecology of floodplain herpetofauna as ‘understudied’ and ‘largely unknown’.

In summary, hydrological processes are known to influence the ecology of flora and fauna. However, understanding how these processes affect amphibian ecology is still in its infancy. A few studies exist on the affects of hydrological cycles on amphibian physiology, diet and population for select species.

1.15 Amphibian Populations, Ecology and Global Decline

Global changes in the phenology and population structure of amphibians have been noticed since the 1970’s (Beebee 1995; Blaustein *et al.* 2001) but records of declines were first postulated at the 1st World Congress of Herpetology in 1989 (Wyman 1990). By 1993 more than 500 populations of frogs and salamanders were listed as of conservation concern or declining (Vial & Saylor 1993). Following further research there is now a consensus among herpetologists that declines have occurred and are likely to continue (Blaustein *et al.* 1994b; Kuzmin 1994; Pechman & Wake 1997;

Waldman & Tocher 1998; Houlahan *et al.* 2000; Semlitsch 2003; Gascon *et al.* 2007). During their lifecycles most amphibians use terrestrial and aquatic environments and due to their permeable skin may be more sensitive than other vertebrates to pollutants or alterations in temperature and rainfall (Duellman & Trueb 1986; Blaustein & Wake 1990; Wells 2007). These biological sensitivities promote amphibians as useful bioindicators of environmental degradation (Weygoldt 1989; Vitt *et al.* 1990; Blaustein *et al.* 1994b; Halliday 2000).

Declines in numbers and diversity for temperate climates are well documented and have been reviewed by Blaustein & Wake (1995), Hecnar & M'Closkey (1996b), Houlahan *et al.* (2000), Blaustein & Kiesecker (2002), Collins & Storfer (2003) and Beebee & Griffiths (2005). Declines for North America and Europe have been associated with habitat modification and/or fragmentation (Beebee 1996; Green 1997; Funk *et al.* 2005b) and/or with the following causal factors; Acid precipitation (Freda *et al.* 1991; Sparling 1995), UV embryonic degradation (Blaustein *et al.* 1997; Blaustein *et al.* 2003), pollutants (Power *et al.* 1989; Hall & Henry 1992; Carey & Bryant 1995; Linder *et al.* 2003; Blaustein *et al.* 2003), changes in climatic responses (Alexander & Eisheid 2001; Pounds, 2001; Carey & Alexander 2003), introduced biotic interactions (Gamradt & Kats 1996; Kiesecker & Blaustein 1997; Collins & Storfer 2003; Bosch *et al.* 2006) and bacterial, fungal and viral infection (Nyman 1986; Blaustein *et al.* 1994a; Cunningham *et al.* 1996; Kiesecker *et al.* 2000; Johnson *et al.* 2003). Most of the declines documented above show no single cause but usually occur as a combination of the above cases acting in synergy with other environmental stressors, shifts in competition, predator-prey interactions and changes in the dynamics of ecological systems (Long *et al.* 1995; Carey *et al.* 2001; Kiesecker *et al.* 2000; Blaustein & Kiesecker 2002; Collins & Storfer 2003).

1.16 Tropical Amphibian Declines

Lips *et al.* (2005a) and Lips *et al.* (2005b) reviewed the theories and current concepts of amphibian decline in Latin America and summarised the anthropogenic and natural mechanisms causing population crashes in the neotropics. Table 1.16.1 lists some of the current status and threats to each country.

Table 1.16.1 Status and literature of neotropical declines (adapted from Young *et al.* [2001] with additions from further research [referenced in table]).

Country	Status / Family / Timing	Source
Mexico	16 sp. in decline, 1 extinct, 38 critically endangered / Hylidae / 1980's	Young <i>et al.</i> (2001); Lips <i>et al.</i> (2004)
Guatemala	3 sp. potentially extinct, 10 critically endangered / Leptodactylidae & Hylidae / 1985-86	Mendelson <i>et al.</i> (2004)
Honduras	9 of 16 sp. affected, 4 extinct, 2 verified, 22 critically endangered / Leptodactylidae, Hylidae, Ranidae, Bufonidae / early 1990's	Wilson & McCrane (1998)
Belize	1 sp. critically endangered, 2 vulnerable.	Young <i>et al.</i> (2003)
El Salvador	1 sp. critically endangered, 2 endangered.	Young <i>et al.</i> (2003)
Nicaragua	Largely unknown status, 2 sp. endangered 4 vulnerable.	Young <i>et al.</i> (2003)
Costa Rica	<i>Monteverdi region</i> ; 20 of 50 sp. absent, 1 extinct; <i>Talamanca Region</i> ; 35 of 51 sp. absent, 1 sp. extirpated. 1 sp. in decline, 15 critically endangered/ Plethodontidae, Leptodactylidae, Hylidae, Bufonidae, Ranidae / 1980's	Pounds & Crump (1994); Pounds <i>et al.</i> (1997; 1999); Lips (1998; 2003a)
Panama	35 of 55 sp. absent, 8 critically endangered / Hylidae, Leptodactylidae, Bufonidae, Ranidae / 1996-97	Lips (1999)
Puerto Rico	3 sp. extinct, 6 declining / Leptodactylidae / 1974-94	Joglar & Burrowes (1996); Burrowes <i>et al.</i> (2004)
Dominican Republic	6 sp. extinct / Bufonidae, Leptodactylidae, Hylidae / 1970-1990	Hedges (1993)
Venezuela	7 of 8 <i>Atelopus</i> sp. extinct / Bufonidae / late 1980's	La Marca & Lötters (1997); Bonaccorso <i>et al.</i> (2003)
Colombia	Local die offs / Leptodactylidae / Hylidae, 1997	Lynch & Grant (1998)
Ecuador	15 sp. extinct, 8 sp. declining / Hylidae, Bufonidae / 1980's	Lötters <i>et al.</i> (2004); Ron <i>et al.</i> (2003; 2001-2004); Pounds <i>et al.</i> (2006)
Peru	8 sp. declining / Bufonidae, Dendrobatidae, Hylidae / no data	Salas (1995)
Brazil	13 of 76 sp. across areas extirpated, 1 montane sp. declining / Leptodactylidae, Hylidae / late 1970's to mid 1980's	Heyer <i>et al.</i> (1988); Funk & Mills (2003); Eterovick <i>et al.</i> (2005); Carnaval <i>et al.</i> (2006)
Chile	1 sp. declining / <i>Rhinoderma</i> sp. / late 1980's -1990's	Young <i>et al.</i> (2001)
Argentina	Unknown status	Vaira (2002)
Note; For further details of exact genus and further specialist groups affected, see Young <i>et al.</i> (2001).		

Forest fragmentation and modification effects on the biodiversity of neotropical habitats are well documented (Goldsmith 1998; Walker 1999) and are slowly beginning to be fully understood through the re-analysis of long-term data (Terborgh *et al.* 1996; Meyer *et al.* 1998; Battersby 1999; Carlson & Edenham 2000; Loh 2000; Brodman 2002; Laurance *et al.* 2002; Alcala *et al.* 2004; Funk *et al.* 2005b; Gardner *et al.* 2007b).

There is clear evidence that an emerging infectious disease, chytridiomycosis, is fast becoming a global pathogen of amphibians that could reach epidemic proportions (Berger *et al.* 1998; Kiesecker *et al.* 2000; Daszak *et al.* 2003). Chytridiomycosis is a fungal disease first described in 1998 from moribund and dead adult amphibians collected in tropical Australia and Panama from 1993 to 1998 (Berger *et al.* 1998). Chytrids are ubiquitous single celled fungi that develop without hyphae and are found in aquatic habitats and moist soil, where they degrade cellulose, chitin and keratin (Powell 1993). The pathogen is the only example of a chytrid that parasitizes amphibians (Berger *et al.* 1998; 1999).

Studies have shown that removal of trees from sensitive areas (i.e. those with less hardy, endemic species) can alter the species composition of amphibians within tropical forests (Heang *et al.* 1996; Pearman 1997; Vitt & Caldwell 2001; Jaafar *et al.* 2002; Ernst & Rödel 2005; Cushman 2006; Gardner *et al.* 2007a). The results of these findings strengthen evidence toward a need for protecting tropical forests. However, even protected reserves that appear safe are at risk and have exhibited declines (Pounds *et al.* 1997; Lips 1999). These declines in pristine undisturbed tropical habitats have been more difficult to elucidate (Richards *et al.* 1993; Lips 1998; Alford *et al.* 2001).

The chytrid pathogen responsible for declines in the neotropics is *Batrachochytrium dendrobatidis*. It kills adult frogs possibly by disruption of homeostasis and kills tadpoles by dissolving the keratinaceous mouth parts, thus starving the tadpoles of food and development (Berger *et al.* 1998). *B. dendrobatidis* is considered an epizootic threat in the neotropics (Daszak *et al.* 2000; 2003) and exhibits a strong potential to spread throughout Latin America, across a wide range of environmental conditions (Ron 2005). Most neotropical regions where *B. dendrobatidis* has been

found have experienced amphibian population declines. These regions include the highlands of Costa Rica and Panama, the Venezuelan Andes, the Ecuadorian Andes, Puerto Rico, highlands of the western nuclear Central America, and the Sierra Madre del Sur of Guerrero, Mexico (La Marca & Lötters 1997; Berger *et al.* 1998; Lips 1998, 1999; Campbell 1999; Ron & Merino-Viteri 2000; Merino-Viteri 2001; Bonaccorso *et al.* 2003; Lips *et al.* 2003a; 2004; Ron *et al.* 2003; Wilson & McCrane 2003; Burrowes *et al.* 2004; La Marca *et al.* 2005).

In Costa Rica *Batrachochytrium dendrobatidis* has been identified in museum collections and is likely to be distributed ubiquitously in the country and a contributor to amphibian declines (Puschendorf *et al.* 2006). Further south in Panama *B. dendrobatidis* has invaded some regions causing an epizootic (Lips *et al.* 2006) and is likely to be still colonising uninhabited areas, including those that have never been documented or surveyed.

Climate change has been implicated in declines of some neotropical amphibians (Pounds *et al.* 1999). It was first identified as a crucial component of tropical amphibian declines in the rapid extinction of the Golden Toad (*Bufo periglenes*) in Costa Rica (Pounds & Crump 1994). Later, in montane regions of Panama, where population crashes were also observed, declines were linked to changes in annual patterns caused by anthropogenic changes in forest dynamics combined with El Nino weather conditions in the south Pacific (Pounds *et al.* 1997). Temperature and moisture strongly influence the ecology and biology of amphibians and scientists have therefore focused climate change studies on the effects of environmental factors in tropical amphibian population biology (Pounds *et al.* 1999; Alexander & Eischeid 2001). While records of climate change effects on other biota flourish (Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003), clear examples of direct links between individual species mortality, population declines and climate change for amphibians are still lacking (Alexander & Eischeid 2001).

A few studies on the synergistic affects of climate change and other known decline factors are slowly being conducted (Carey *et al.* 2001; Carey & Alexander 2003; Lewis 2006). Pounds *et al.* (2006) have recently made a clear link between climate fluctuation and the presence and spread of chytridiomycosis in Ecuador. Bernado &

Spolita (2006) have discovered a concrete example of climate change affecting a population of montane salamanders. They suggest that amphibians inhabiting specialist forest niches are likely to be physiologically limited in range by their natural thermal tolerances. Climate change thus forces the salamanders out of range in search of more comfortable conditions, altering their population dynamics radically (Spolita 2006). Lips *et al.* (2003b) have identified a series of correlates for declining amphibians in Central America that include patterns of decline, habitat associations, morphological and topographical similarities. Further study into these correlates could reveal common mechanisms in declines that would help create predictive models that could recognise decline patterns before they occur.

The case for understanding and solving tropical amphibian declines continues to become ever more urgent. Although remedies for some issues are being sought, the implications for the immediate loss of some widespread species could have catastrophic consequences. Whiles *et al.* (2006) collated decline causes and suggest that mortality in tropical amphibians at current rates and magnitude would have a larger scale effect on many higher organisms at an ecosystem level. There is even data that suggests that mortality of tropical amphibians could result in vast increases of lower invertebrate prey items. Population explosions in some insect species could alter ecosystem processes radically (Wyman 1998; Beard *et al.* 2003).

1.17 Environmental Affects to Amphibians

1.17.1 Climate

Some temperate species of fauna have exhibited poleward shifts in range and/or changes in phenology and breeding habits (Parmesan 1996; Gitay *et al.* 2002; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003). Models have been created that suggest climate shifts could be impacting species by altering population size, range size, breeding timing, species composition, preferred habitat, prey resource and ultimately, survival probability (Carey *et al.* 2001; Peterson *et al.* 2002; Pearson & Dawson 2003; Thomas *et al.* 2004).

For amphibians, some populations have been positively correlated to stress by climate change, but others appear stable, or have demonstrated a capacity to respond behaviourally and physiologically in novel ways (Parmesan 1996; Pounds *et al.* 1999; Alexander & Eischeid 2001; Blaustein *et al.* 2001; Bernado & Spotila 2006).

Amphibians in North America and Europe have been affected in their breeding phenology, calling behaviour and activity patterns since the 1970's and research has concluded that some declines are due to habitats gradually desiccating (Beebee 1995; Drost & Fellers 1996; Ovaska 1997; Gibbs & Breisch 2001; Tryjanowski *et al.* 2003; Araújo *et al.* 2006). In tropical latitudes, climate change effects on amphibians have been more difficult to elucidate and only recently has the phenomenon been positively identified as a contributory agent that acts in synergy with other decline agents (Pounds *et al.* 1999; Alexander & Eischeid 2001; Carey *et al.* 2001; Pounds *et al.* 2006).

At a component level, temperature fluctuations are slowly being recognised as a contributory factor in cases of amphibian decline, both locally and globally (Stewart 1995; Pounds *et al.* 1999; Kiesecker *et al.* 2000; Blaustein *et al.* 2001; Carey & Alexander 2003; Corn 2005). Tropical temperatures are known to correlate with daily amphibian activity patterns (Duellman 1982; Donnelly & Guyer 1994; Duellman & Trueb 1986) and can restrict certain amphibian species to certain habitats and regions (Duellman 1982). This can also explain why some species are inactive during certain periods in the tropics (Duellman 1982). Alterations in normal ambient temperature and humidity were the first tropical climate components to show correlation with negative change in amphibian activity. This eventually led to consequential affects in population fluctuations (Pounds & Crump 1994; Pounds *et al.* 1999).

1.17.2 Precipitation

Rainfall patterns are also correlated with amphibian activity and breeding phenology in tropical environments (Duellman & Trueb 1986; Guyer 1994; Pearman 1997; Bertoluci 1998; Donnelly & Guyer 1994; Stebbins & Cohen 1995; Pearman 1997; Schlaepfer & Gavin 2001). Rainfall can directly influence amphibian physiological activity patterns and restrict them to certain habitats and regions (Duellman 1982). Rainfall can give an indication of their daily behaviour and may also explain why

certain species are inactive during certain periods. Rainfall is an important variable at Caño Palma as heavy rainfall in November marks the onset of the main amphibian breeding season.

1.17.3 Ambient Wind

Wind speed has been shown to influence amphibian activity patterns, although usually in synergy with rainfall and temperature change. Its affects are largely due to amphibian's ectothermic nature and physiological susceptibility to water loss if exposed to wind currents (Crump 1994; Donnelly & Crump 1998; Alexander & Eischeid 2001; Bernado & Spotila 2006).

1.17.4 Water Chemical Composition

Due to their semi-aquatic habits, and porous skin, amphibians are affected by water they submerge themselves in, whether for breeding, or because certain species are solely aquatic (Duellman & Trueb 1986). Amphibians that use aquatic habitats are therefore also susceptible to alterations in the chemical and physical composition of water (Linder *et al.* 2003). They have even been suggested to be as sensitive to pollution as fish (Linder *et al.* 2003). Numerous studies have investigated the mechanisms and susceptibility of amphibians to aqueous pollution (Linder *et al.* 2003). The key pollutants affecting amphibians include pesticides (Hall & Henry 1992), fertilisers (Hatch & Blaustein 2003), heavy metals (Horne & Dunson 1994), acidification (Pierce 1986; Freda *et al.* 1991) and effluent level changes in water (Power *et al.* 1989). Chemical imbalances and nutrient fluctuation in water can also alter the quality of an amphibian breeding site (Duellman & Trueb 1986). The physiological condition and survivability of adults and larvae can be subsequently affected (Hecnar & M'Closkey 1996a; Stebbins & Cohen 1995; Linder *et al.* 2003; Kaufman 2005).

1.17.4.1 pH of Water

pH can affect amphibian presence, diversity and metamorphic development in water bodies where atmospheric sulphur dioxide pollution has occurred or where geological

features create naturally high or low pH levels (Golterman 1969; Pierce 1986; Freda *et al.* 1991). Some amphibian species show preference for a higher, more alkaline pH in the water bodies they inhabit, whereas others thrive in more acidic conditions (Pierce 1986; Linder *et al.* 2003). The pH of most rainfall that falls into ponds used by amphibians is approximately 6.0 or in some cases 5.0 due to water droplets collecting Carbon Dioxide (CO₂) when falling to the ground (Harrison 1992). An aquatic pH of about 6 to 9 is favoured by the majority of freshwater life, especially fish and amphibians (Duellman & Trueb 1986).

1.17.4.2 Conductivity of Water

Specific conductivity is a measure of how much electrical current can pass through water and is related to the concentration of ions. Ions that influence conductivity include; inorganic dissolved solids, such as chloride, nitrate, sulphate and phosphate anions (i.e. negative ions), sodium, magnesium, calcium, iron and aluminium cations (i.e. positive ions). Conductivity is affected by water temperature; the warmer the water, the higher the conductivity. It is measured in Siemens per meter (mS) or micromhos (μmho) and is useful as a general measure of water quality. It can indicate concentrations of dissolved inorganic matter which in turn can indicate presence of metals (Hunt & Wilson 1986). Conductivity in streams and rivers is affected by the geology of the area. Presence of sodium chloride in tidal water also increases conductivity with increasing salinity. All water tends to have a relatively constant conductivity that can be used as a baseline for comparison. Significant changes in conductivity can be used as an indicator of pollution entering a stream (Harrison 1992).

1.17.4.3 Ferrous Iron in Water

Iron is a common element found in natural aquatic environments. It is a dietary component for most organisms, and is a factor that affects water organisms in surface layers (Thompson *et al.* 2005). Iron exists in water in two types, bi-valent (ferrous iron - Fe²⁺) and tri-valent (ferric iron - Fe³⁺). Waters of high alkalinity often have lower iron content than acidic waters. The commonest form in which iron is found in water is as ferrous bicarbonate - a soluble, colourless salt that exists only in solution.

When in the presence of organic substances, ferrous iron induces the formation of organic complexes which increase its solubility in water. Organic ferrous iron is iron combined with organic matter and is sometimes called tannin or lignin, typically when it is made up of plant matter. Water that contains small quantities of organic ferrous iron in the form of tannins and lignin are usually stained and dark in colour. Such water is a characteristic of the Caño Palma and other blackwater canals in the neotropics.

Ferric iron forms complexes of hydroxides when in solution and is often coupled with other inorganic complexes with substantial bicarbonate, sulphate, phosphate, cyanide or halide content. Its solubility in water is increased by rising levels of carbon dioxide and decreasing pH. Some non-organic anthropogenic iron compounds are also present in water as ferric iron, and when these become soluble, they can be toxic to aquatic biota (Thompson *et al.* 2005).

Non-organic anthropogenic metals, including non-organic ferric iron (Freda 1991), are known to be toxic to amphibians, causing problems in development, survival (Horne & Dunson 1994; Linder *et al.* 2003; Snodgrass *et al.* 2005; Roe *et al.* 2006) and immune system dysfunction (Fink & Salibián 2005; Fournier *et al.* 2005). Most of these metals tend to be strongly adsorbed by soil constituents, especially organic matter (Brady & Weil 2007). Their mobility in the environment and bioavailability depends on the soil organic matter content, pH and redox potential. The effects of ferric iron on amphibians can include genotoxicity at concentrations above 4.5mg/l (Godet *et al.* 1987) and alterations to red cell ferritin, the main protein that stores iron for organs that need it, especially the liver and the bone marrow where red blood cells are made (Shull & Theil 1982; Dickey *et al.* 1987). Changes in red cell ferritin can interfere with ontogeny in larval amphibia (Schaefer & Theil 1981).

Increases in ferrous iron levels can indicate sudden availability of additional ferric iron compounds that have become solute and indicate a possible contamination by heavy metals in water. By monitoring natural ferrous iron levels in water, any heavy fluctuations can be detected.

1.17.4.4 Nitrate in Water

Nitrogen is necessary for both terrestrial and aquatic plant growth. In water it is derived from a variety of sources, including decomposition of organic material, wastewater, industrial sources, man-made fertilizers and sewage (Broomhall 2005). While excessive nutrients can cause undesirable, deleterious plant growth, an appropriate level of nitrogen is a succession component of an aquatic ecosystem. Nitrogen ends up in the environment mainly through agricultural processes, and thereby also ends up in water. The main source of nitrogen in water is fertilizers that occur as nitrate nitrogen. However, ammonia, ammonium, urea and amines also end up in water from fertilizers. The most widely applied nitrogen fertilizers are probably NaNO_3 (sodium nitrate) and NH_4NO_3 (ammonium nitrate) (Hellawell 1986). After fertilizers are applied the crops take up as little as 25-30% of added nitrogen compounds (Hill 1991; Soffe 1995). The residue often ends up in groundwater and surface water from soil leaching because nitrates are water soluble (Hill 1991).

Determining optimum levels of nitrates in water is complex. Their levels fluctuate because of constant uptake and release by aquatic life, exchanges in stream sediment, and various other transformations. Natural nitrate rarely exceeds 10mg/l and is usually less than 1.0mg/l. Concentrations greater than 20mg/l pose a health hazard to animals as they can reduce blood's haemoglobin and ability to transport oxygen. High blood concentrations can also become cancerous (Burt *et al.* 1993).

Nitrate can kill amphibians by direct contact at concentrations equal to and less than those applied for agriculture purposes (i.e. 5-500mg/l) (Hecnar 1995; Oldham *et al.* 1997; Marco *et al.* 1999; Rouse *et al.* 2001; Smith *et al.* 2005; Burgett *et al.* 2007). It can also alter their behaviour, feeding habits and prey abundance (Hatch 2001). However, several insitu experiments of nitrate runoff affects on amphibians have shown that in natural conditions when nitrate is applied to and mixed with soil it does not affect some adult amphibians but can interfere with larval ontogeny (Watt & Oldham 1995; Johansson *et al.* 2001; Wijer *et al.* 2003), especially when larvae are exposed to high UV-B radiation (Hatch & Blaustein 2003).

Nitrate can also seriously alter the vegetation balance in a pond by eutrophication, subsequently choking the pond with vegetation and negating its suitability for pond breeding amphibia (Johansson *et al.* 2001; Wijer *et al.* 2003; Linder *et al.* 2003; Massal *et al.* 2007).

1.17.4.5 Hardness of Water (dH)

Hard water is water that has high mineral content (in contrast to soft water). It is also known as the capacity of water for destroying a lather of soap and is caused by minerals in solution. Hard water minerals primarily consist of calcium (Ca^{2+}), and magnesium (Mg^{2+}) metal cations, and sometimes other dissolved compounds such as bicarbonates and sulfates. Calcium usually enters water as either calcium carbonate (CaCO_3), in the form of limestone and chalk, or calcium sulfate (CaSO_4), in the form of other mineral deposits. Hard water is generally not harmful and is mostly due to the underlying geology of the sample. It is usually expressed as mg/l CaCO_3 and therefore can also be correlated with increases in alkalinity (Brown *et al.* 1997).

Hard water can be measured in a number of units. One of the most commonly recognised units is the German degree of hardness or Deutsche Härte (dH). One degree of dH is defined as 10 milligrams of calcium oxide (CaO) per litre of water, which is equivalent to 17.848 milligrams of calcium carbonate per litre of water, or 17.848mg/l. Using the dH scale water can be categorised as very soft (0-70mg/l), soft (70-150mg/l), slightly hard (150-250mg/l), moderately hard (250-350mg/l), hard (320-420mg/l) and very hard (420mg/l and above).

Studies on the affects of hardness on amphibians are few, probably because it is unlikely to physiologically affect adult amphibians due to such subtle differences in CaCO_3 . However, it is considered an aspect of water quality that has an influence over habitat choice by pond breeding amphibians (Duellman & Trueb 1986; Godfrey & Sanders 2004). Hard water is also a measure that is correlated with increased toxicity to heavy metals in amphibians and therefore it can be a useful indicator for pollution by heavy metals in aquatic ecosystems (Horne & Dunson 1996; Stubblefield *et al.* 1997).

1.17.4.6 Oxygen in Water

Dissolved oxygen (DO) is oxygen (O₂) that is dissolved in water. The amount of DO present naturally in water is affected by atmospheric pressure, ion activity, bacteria levels, fertilisation of plants and temperature (cold water contains more DO than warm water). DO is necessary in aquatic ecosystems for survival and growth of flora and fauna. It is also an indicator of ecosystem health. Accurate data on DO concentration in water is essential for identifying changes that result from natural and anthropogenic phenomena. How much DO an aquatic organism needs depends upon the species, its physical state, pollutants and environmental factors. Amphibians, like fish, are poikilothermic so they use more oxygen at higher temperatures due to their metabolism increasing (Duellman & Trueb 1986; Wells 2007). Numerous scientific studies suggest that 4-5mg/l DO in water is the minimum that will support a large, diverse fish population. The DO level in healthy fish populated waters generally averages about 9.0mg/l (Harrison 1992).

Amphibians require similar levels of aqueous oxygen as fish to live in water. However, dermal oxygen absorption, combined with the use of a primitive lung or lungs allow many amphibia to exist in aqueous environments with oxygen levels below that what a fish would require (Withers & Hillman 1983; Duellman & Trueb 1986). Amphibians have even evolved mechanisms to cope with lower aquatic oxygen levels in their lifecycles. Egg masses can swell in size to increase surface area for oxygen absorption or diffuse with specific algae to correct hypoxia (Pinder & Frier 1994; Mills *et al.* 2001). Some larval amphibia have branched gills allowing enhanced oxygen exchange in water (Wells 2007). Most juveniles and many adults have a primitive lung they use to breath in combination with their osmotic skin (Duellman & Trueb 1986). Adults can also physiologically decide on pond condition by aqueous chemical signals (Wells 2007).

Studies on environmental fluctuation of DO levels on amphibia are scarce (Wells 2007). Most that do exist have concentrated on specific species (Ultsch 1971) or have recorded DO levels are part of more general habitat monitoring (see Wells 2007 for a summary) with only a few documenting daily or regular seasonal variation (Ultsch 1971; Bradford 1983; Wong & Booth 1994; Nie *et al.* 1999). Although oxygen is

seldom a limiting factor for amphibians (Wells 2007), aquatic environments can present less favourable conditions for amphibians when DO levels become affected by or change because of altered temperature, water column mixing, flow rates, depth, vegetation cover, bacterial respiration and pollution (Talling & Lemoalle 1998).

1.17.4.7 Carbon Dioxide in Water

Almost all natural water contains CO₂ gained by precipitation as absorbed CO₂ gas from the air and rainwater. On reaching the earth, rainwater is slightly acid and will absorb CO₂ if it flows through decaying vegetation. Aquatic plant life depends on CO₂ in water for growth and in the photosynthesis of starches, sugars, oils and proteins. Although CO₂ itself is not especially detrimental to amphibia (Wells 2007), rises in concentrations in water can make it difficult for fish and amphibians to use limited oxygen present (Harrison 1992). If the oxygen/CO₂ balance is disturbed by heavy effluent, metal, pesticide or other pollution, CO₂ levels can become severely affected, and kill amphibians by creating anoxic conditions (a lack of oxygen).

The effect of increased CO₂ levels on amphibians have been included in studies dealing with oxygen levels and CO₂ osmosis (e.g. Ultsch 1976). High CO₂ levels can impede elimination of CO₂ through the skin and result in acidosis. Some amphibians such as aquatic Sirens (*Pseudobranchius striatus*) can survive higher levels of CO₂ than fish but other amphibia are much less studied. Unknown direct effects of carbon accumulation on amphibians as dissolved organic carbon (DOC) also exist, which has recently been proven to bio-accumulate in the food chain (Chen *et al.* 2000). Swamp environments generally have higher levels of naturally occurring CO₂ due in part to low levels of dissolved oxygen (DO). Both low levels of DO and high levels of CO₂ often fluctuate in synergy (Talling & Lemoalle 1998).

1.17.4.8 Saline Water

Salinity is the term describing the presence of sodium chloride, magnesium and calcium sulphates that occur in water. Salinity is an ecological factor of importance, influencing the types of plants and organisms that live in a body of water (Brönmark & Hansson 2005). Salinity in ground water is indicated by; a ground surface that has

become permanently or seasonally waterlogged, damp remaining after extended rain, intermittent streams that flow for long periods, dieback of vegetation in low lying areas, failure of plants to germinate or grow, areas of bare soil, increase in salt-tolerant plants in an area, changing pasture composition, reduced diversity, deterioration in the quality of groundwater, and rising water levels in bores (Talling & Lemoalle 1998).

Amphibians are generally freshwater vertebrates and as such are poor osmoregulators of salt (Duellman & Trueb 1986; Boutilier *et al.* 1992). They are known to be affected by salts physiologically during reproduction and morphological development. It is less known that they are affected by increases in salinity in their environment that affect their prey and resource abundance (Christy & Dickman 2002; Gomez-Mestre *et al.* 2004; Lane *et al.* 2007). Consequently, the majority of amphibian species avoid inhabiting and breeding in saline and brackish environments (Balinsky 1981).

1.17.5 Pollution Risk at Caño Palma

The natural quality of rivers, streams and canals is reflected in the quality of upstream surface run-off and groundwater discharge (Harrison 1992). Along tropical waterbodies, people live in the riparian boundary (Junk *et al.* 2000), and it is here, where land is cultivated for agriculture and industry, that waste can accumulate in water systems (Brönmark & Hansson 2005). In recent years agriculture for Bananas in the northeast lowlands of Costa Rica has created polluted run-off that has drained via river systems into the Tortuguero region. Some studies of the run-off have shown that stirring of settled sediments by tides has the potential to place aquatic organisms at risk from pollution by nitrate fertilisers, insecticides and fungicides (Henriques *et al.* 1997; Castillo *et al.* 2000). Due to Caño Palma's coastal location, any of these pollutants flowing downstream from an anthropogenic source have a risk of being returned upstream during spring tides that flood riparian forests.

1.18 Surveying for Tropical Amphibians

Study of amphibian population biology in tropical environments has been more concentrated in recent years due to the increased recognition amphibians have

received from their rapid declines (Halliday 1998; Storfer 2003; Beebee & Griffiths 2005; Norris 2007; Whitfield *et al.* 2007). Despite efforts already made, detailed information pertaining to natural fluctuations in local populations is still relatively understudied and desperately needed (Pechmann & Wilbur 1994; Alford & Richards 1999; Young *et al.* 2001; Young *et al.* 2004; Lips *et al.* 2005b).

This situation is compounded by the many diverse species of amphibians and their complex metapopulations and specialist environments (Alford & Richards 1999; Young *et al.* 2001; Marsh 2001; Smith & Green 2005). The small patches of specialist environment are often where the rarest species exist and where population fluctuation can be highest (Nee *et al.* 1997; Marsh 2001; Smith & Green 2005).

The dynamic population changes at local levels in the tropics requires standardised survey methods and a requirement for multiple year studies of populations to correctly estimate distributional change in amphibians (Blaustein *et al.* 1994b; Pechmann & Wilbur 1994; Marsh 2001; Schmidt 2003; Skelly *et al.* 2003; Dodd & Dorazio 2004; Smith & Green 2005). In order to tailor individual surveys to specialist environments, an understanding of what ‘habitat niches’ are used by amphibians is necessary (Heyer *et al.* 1994).

1.18.1 Pond Habitat Niches

Pond ecosystems provide a framework of metapopulation structure and dynamics for many amphibian species (Blaustein *et al.* 1994b; Pechman & Wilbur 1994; Hecnar & M'Closkey 1996b). Within this framework pond breeding amphibians require different riparian habitats at various stages of their lifecycle depending on their reproductive mode (Wells 2007). For example, an *Agalychnis callidryas* specifically requires overhanging leaves at the edge of a pond to lay egg clutches to, whereas *Rana vaillanti* requires a waterbody with permanence to lay egg spawn clumps into directly (Savage 2002). These habitat niche requirements can influence the population distribution, breeding strategy and spatial distribution of amphibia (Sinsch 1990; Pough *et al.* 1998; Perret *et al.* 2003; Rothermel 2004; Wells 2007). Consideration of riparian zones is therefore vital in surveying a pond breeding species population assemblage (Rothermel 2004; Bosch & Martinez-Solano 2003).

Studies on anuran pond communities in the Atlantic tropical rainforest have increased steadily in the last 20 years (e.g. Scott 1976; Crump 1974; Toft 1980; Aichinger 1987; Donnelly 1994; Bertoluci 1998; Eterovick & Sazima 2000; Bertoluci & Rodrigues 2002; Abrunhosa *et al.* 2006). However, the number of studies conducted on temporary and disturbed ponds and their riparian habitat is still far below the number of studies treating permanent ponds. The former studies have focused on reproductive aspects related to the hydroperiod of a pond. These include investigations into tadpole phenotypic plasticity (e.g. Tejedo & Reques 1994; Blaustein *et al.* 1999) and anuran succession (i.e. species composition and temporal resource, species arrival, chorus attendance and tadpole phenology [e.g. Dixon & Heyer 1968; Heyer 1973]). Community and population studies on dynamic and disturbed ponds are therefore still required to bridge the gap with settled/permanent pond studies.

1.18.2 Forest Habitat Niches

Globally, amphibians reside in many forest types (Duellman & Trueb 1986; Stebbins & Cohen 1995; Pough *et al.* 1998; Duellman 1999; Young *et al.* 2004; Wells 2007). Often they require several habitat components within forests to develop and mature (Duellman & Trueb 1986; Wells 2007). For terrestrial species the understorey and leaf-litter layer in natural forests provide amphibians with shelter, moisture, insect prey and protection from predators (Duellman & Trueb 1986; Stebbins & Cohen 1995). For arboreal species the canopy can provide all the above in a multi-storey style habitat (Stebbins & Cohen 1995). Both arboreal and terrestrial habitats provide preferred humidity and temperature conditions that amphibians need for their ectothermic lifestyle (Brattstrom 1979; Sinsch 1984; Kaul & Shoemaker 1989; Moore & Sievert 2001).

Many anuran amphibians also require both aquatic and terrestrial habitats to complete their lifecycle (Duellman & Trueb 1986; Hermann *et al.* 2005; Wells 2007). For example, Leopard Frogs (*Rana pipiens*) in North America require three different habitats throughout the year; breeding ponds in spring, grassy meadows for summer foraging, and lakes or streams for overwintering (Pope *et al.* 2000). Therefore areas of forest without temporary or permanent water bodies do not always fulfill all the

habitat requirements of resident amphibians (Lecis & Norris 2003; Hermann *et al.* 2005). In the tropics, where forests have more dynamic niches, amphibians have evolved a whole range of specialised behaviours and mechanisms that enable them to survive and breed in forest environments (Crump 1974; Pough *et al.* 1998; Wells 2007). These specialist habits vary between local areas and along forest gradients as well as at national levels, thus making identification of niche forest use by amphibians ever more important in understanding their ecology (Duellman 1988; Duellman 1999; Savage 2002).

1.19 Methods of Surveying for Tropical Amphibians

The higher diversity in tropical environments has maximised the niche options for amphibians (Stebbins & Cohen 1995; Savage 2002; Wells 2007). Such diversity also promotes interspecific competition for natural resources and this thus attracts a range of predators ensuring species evolve cryptic abilities that complicates locating them in their natural environment (Stebbins & Cohen 1995; Savage 2002; Wells 2007). As a result of this difficulty researchers have devised numerous survey methods for detection ranging from visual encounter, indirect signs and trapping, each with merit for specific species (Heyer *et al.* 1994; Pearman *et al.* 1995; Parris 1999; Rodda *et al.* 2001; Doan 2003; Rödel & Ernst 2004; Hsu *et al.* 2005; Woolbright 2005).

1.19.1 Visual Encounter Surveys (VES)

VES is a successful and proven technique for amphibian population monitoring in tropical environments (Doan 2003; Rödel & Ernst 2004; Rodda *et al.* 2001; 2005). VES can be performed over transects and involves visual inspection of terrestrial and gallery vegetation for species both nocturnally and diurnally. The technique involves walking a slow pace along a line transect and recording the sighting of amphibians that are resting or moving in visual proximity. All niches on the transect line are inspected and include features like leaf-litter, branches, leaves, tree buttress, tree fall or vines. VES can be either timed or area constrained for standardisation and this can be varied depending on the goals of a study (Vonesh *et al.* 2010). It is a useful technique for creating rapid species lists and detection for most amphibians (Crump & Scott 1994; Rodda *et al.* 2005).

Some amphibians are easier to survey by VES than others (Vonesh *et al.* 2010). This is often due to variation in their conspicuousness and niche habitat selection. Fossorial species or high canopy dwellers, for example, are not well suited to VES and different techniques must be deployed to capture these species. The analysis of VES data relies on the following assumptions;

- 1) All individuals have equal detectability.
- 2) Individuals are recorded once during a survey.
- 3) There are no observer related biases.

In most survey instances the above limitations will in some way occur. Amphibians of different species, sizes or life stages are generally not equally conspicuous and detection probabilities among amphibians can vary considerably (Schmidt 2005; Mazerolle *et al.* 2007; Vonesh *et al.* 2010). Given these limitations, VES is best considered a qualitative or semi-quantitative survey method. However, it can bolster stronger techniques like quantitative quadrat surveying, if the data is part of a mark-recapture scheme. Unlike simple abundance counts, mark-recapture data makes allowances for detection variation and would not necessarily fail in the above three limitations (Williams *et al.* 2002; Vonesh *et al.* 2010; see 1.20.1).

1.19.2 Leaf-Litter Quadrats

Quadrat sampling has successfully been employed in tropical forests to determine spatial density, diversity and relative abundance of amphibians (Lloyd *et al.* 1968; Scott 1976; Inger 1980; Lieberman 1986; Jaeger & Inger 1994; Rocha *et al.* 2001). It can account for fossorial species, arboreal species that are known to rest in leaf-litter (i.e. *Pristimantis diastema*), and can deal with habitat heterogeneity when sampling for multiple species with different microhabitat preferences.

The technique is statistically superior when sampling before and after comparisons, compared with other quantitative techniques, and statistically strong when used in combination with techniques like VES (Heyer *et al.* 1994; Rocha *et al.* 2001; Doan 2003; Funk *et al.* 2003). Although intensive, the technique brings the surveyor within

easy identification and catching distance of target amphibians. Previous studies have shown that 50-100 quadrats is sufficient enough to cover a 1000 x 1000m area (Inger 1980; Jaeger & Inger 1994), although this is time dependent on the resulting number of amphibians per quadrat. Species densities may vary between areas. An asymptote for means of amphibians/quadrat has been proven to be between 50 and 100 quadrats, even for results exhibiting low density (Lloyd *et al.* 1968).

1.19.3 Trapping Methods

Trapping methods for amphibians fall into two general categories - passive traps (those that actually trap animals) and active traps (those that attract animals but require an observer to capture them). The most popular of these methods are pitfall traps, funnel traps (or variants of such as pipe traps) and coverboards/artificial cover objects (ACOs). For a review see Heyer *et al.* (1994) and Wilson & Gibbons (2010). In most terrestrial and some aquatic circumstances vertically installed barriers (drift fences) can intercept passing amphibians and guide them into traps faster and easier, by increasing the surface area that traps are operating in (Friend *et al.* 1989; Wilson & Gibbons 2010).

Trapping has been used effectively in many countries for a range of amphibian species (mostly terrestrial) (Friend *et al.* 1989; Jehle *et al.* 1005; Weddelling *et al.* 2004). However, trapping has not always been successful in the tropics (Hsu *et al.* 1985; Parris *et al.* 1999). This is possibly because many tropical species are arboreal or semi-arboreal, do not migrate long distances from home ranges, or occupy a semi-fossorial niches that restrict movements over distances that would enable easy capture (Wells 2007).

Both active and passive traps can be monitored on nearly any temporal schedule and timing of surveys can reflect specific questions of interest. However, comparing samples may often require that they are gathered during consistent environmental conditions so as not to bias detectability (Wilson & Gibbons 2010). Because active traps yield high capture rates of target species they can be useful for assessing specific patterns of abundance over time or space. Some of the limiting factors in trapping are access to, and delivery of, materials for trapping, labour intensive layout of project

(studies can only realistically be assessed with adequately high density of traps), and an assumption that capture probability is equal for all target species (Schmidt 2005; Wilson & Gibbons 2010).

1.20 Estimating Tropical Amphibian Populations

1.20.1 Mark-Recapture (M-RC)

Mark-recapture has long been used as an estimator for populations (Southwood 1978; Begon 1979). The foundation of the method was first used for ecological study by Petersen (1896) to estimate Plaice flatfish (*Platichthys platessa*) populations. Later, Lincoln (1930) independently developed the method to estimate waterfowl populations.

The principle used to calculate population size in these early studies still applies. If a sample from a population is marked, returned to the original population and then, after complete mixing, is re-sampled, the number of marked individuals in the second sample would have the same ratio to the total numbers in the second sample, as the total of marked individuals originally released would have to the total population. Since Petersen and Lincoln's first uses, studies and techniques for specific organisms has flourished and are reviewed by Eberhardt *et al.* (1979) for marine mammals, Nichols *et al.* (1981) for birds, Nichols *et al.* (1984) for small mammals, Burnham *et al.* (1987) and Pine *et al.* (2003) for fish, and Kendall *et al.* (1997) for amphibians.

M-RC has been used by herpetologists since the 1920s to analyse species in a variety of habitats (Heyer *et al.* 1994). It is now regarded as the most quantitatively powerful technique for monitoring amphibian populations (Blaustein *et al.* 1994b; Alford & Richards 1999; Funk *et al.* 2003).

Techniques of M-RC for amphibians involve the marking and subsequent release of individuals from a sample or subset of the population, followed by recapture and identification from at least two further sampling sessions. Sampling and marking can be repeated cyclically and recaptures requiring re-marking can persist in a population

for as long as the study requires or until mortality or migration from the sampling area (Arnason *et al.* 1991; Williams *et al.* 2002; Amstrup *et al.* 2006).

M-RC relies upon the following assumptions;

- The initial sample is representative of the population and not biased (for example by sex or age).
- Animals taken in the initial sample are marked and the marks are permanent for the duration of study.
- The marked animals are released and become distributed randomly in the population.
- The marking technique does not affect the recapture, survival, or normal behaviour of the species.

1.20.1.1 Capture Principles of Mark-Recapture

Handling amphibians for study purposes requires careful planning. Due to their breathable, soft, semi-permeable skin, amphibians of all sizes can die by dehydration in the human hand (Duellman & Trueb 1986; Pough *et al.* 1998). For the purposes of M-RC, handling is necessary to mark and return an individual to its natural habitat alive. Capture and handling success is essential to avoid potential biases in results and prevent accidentally euthanizing a target amphibian (Heyer *et al.* 1994).

To protect the amphibians during study latex gloves can be worn during field work (Plate 1.20.1.1). This minimises both damage to handler and amphibian (with respect to the toxicity of some species and amphibians' fragile skin). Latex gloves also protect against foreign toxins like DEET (diethyltoluamide mosquito repellent) residue that can often be on the hands of an individual prior to survey.

Captures for M-RC should be made as gently as possible. Most species can be captured in the hand by simply closing cupped hands around the amphibian and the leaf or stem that it may be sitting on. Terrestrial species can be caught in the same manner. Some species such as *Rana vaillanti* and some *Leptodactylus* sp. are rapid

leapers and can be caught using a faster, more secure hand capture or by use of a hand net. Amphibians' soft and supple bodies minimise internal damage to the body from capture.

Plate 1.20.1.1 Secure handling of *Chaunus marinus* (Todd Lewis 2004).

All anuran amphibians can be held in the hand securely by unfolding the back legs and holding them outstretched with the index fingers, while supporting the dorsum with the thumb (Plate 1.20.1). This is comfortable for anurans and prevents stressful agitated movement and jumping by the captured individual.

1.20.3 Toe-clipping

Toe-clipping is a method of marking amphibians that involves the removal of a single or number of digits from a hand or foot to give an individual amphibian a unique reference mark. The technique requires a sharp pair of laboratory scissors and alcohol to clean them with. Antibiotic and antifungal creams can be applied to digits to reduce potential infection. It is suggested that larger anurans such as *Chaunus marinus* receive a local anaesthetic prior to digit removal (Heyer *et al.* 1994).

This method has standardised procedures for amphibian biologists and has been proven to cause minimal harm to amphibians as they possess powerful regeneration capabilities that enable them to re-grow limbs (Duellman & Trueb 1986; Lüddecke & Amézquita 1999; Kinkead *et al.* 2006; Phillott *et al.* 2007). A good summary of welfare considerations of toe-clipping is provided by Halliday (1994).

A variety of coding schemes can be used with toe-clipping to individually mark each captured amphibian. The system used in this study originates from Donnelly (1989a) and uses a non-numerical sequence of clipping. The code associated with each toe refers to its foot location (left, right, front, or rear) and toe position (innermost = 1, outermost = 4 or 5). The first 18 animals of a given species have one toe removed (LF = Left front foot, RB = Right back foot). For example; LF1, LF2, LF3, RF1, RF2, RB3, RB4 or RB5. After all the unique one toe combinations have been used then a two toe scheme commences. For example; LF1, RF1; LF1, RF2; LF1, RB2 or LF1, RB2. After all two toe combinations are used then three toe codes can be used. With this system thousands of amphibians can be marked by removing no more than two toes per foot. Other variants of this system are reviewed in Donnelly *et al.* (1994).

Previous studies have debated the minor negative and positive effects on population results using toe-clipping (Golay & Durrer 1994; Lemckert 1996; Reaser & Dexter 1996; Parris & McCarthy 2001; McCarthy & Parris 2004; Funk *et al.* 2005b; Liner *et al.* 2007). Negative opinions of the technique have deduced that toe-clipping reduced the average return rate by 4-11% for each toe removed on the same hand after the first (McCarthy & Parris 2004). However, such results have often been species specific in their conclusions and lacking in statistical power. The study by McCarthy & Parris (2004) was unable to accurately consider species specific differences and losses caused by natural migration and predation.

1.21 Population Modelling of Survey Results

In order to interpret amphibian population fluctuations with an interest toward patterns of decline, an absolute estimate of population size is required. Mark-recapture (M-RC) is considered the main alternative approach to standard count data of

amphibians with the advantage that accuracy does not depend on a fixed unit of habitat (Marsh 2001; Williams *et al.* 2002; Schmidt 2003; Dodd & Dorazio 2004; Smith & Green 2005; Amstrup *et al.* 2006).

M-RC methods are also more advantageous than count data because of their strength in detection probabilities that are variable and <1 (Schmidt 2003; Dodd & Dorazio 2004; Amstrup *et al.* 2006). M-RC provides a strong standard error calculation that can assist in assessing the quality of a population estimate, a feature that weakens the power of count data (Dodd & Dorazio 2004; Schmidt 2004). A particular disadvantage of M-RC is that accuracy often depends on capturing a significant proportion of an amphibian population, but does have the advantage of allowing for miss-captures (Williams *et al.* 2002; Amstrup *et al.* 2006).

Seber (1982), Seber (1986), Seber (1992), Schwarz & Seber (1999), Williams *et al.* (2002), and Amstrup *et al.* (2006) review the statistical theory that underlies the M-RC approach to population modelling. The method was originally developed to estimate population size but is now additionally used for the estimation of species diversity, distribution, birth, death and emigration rates (Seber 1982; Pollock *et al.* 1990, Nichols 1992, Lebreton *et al.* 1992; Boulinier *et al.* 1998; Nichols *et al.* 1998; Williams *et al.* 2002; Schmidt 2003; Schmidt 2004; Amstrup *et al.* 2006).

1.21.1 Choosing a Population Model

Analysis of population data can entail simple methods, for example, total counts of a species in an area, or more complicated methods such as estimating species abundance, survival rates, capture probability and population viability (see Williams *et al.* 2002; Amstrup *et al.* 2006). To study a population as a whole through time by total counts is unfeasible as it would not allow for immigration and emigration through a period of time. Therefore, in order to study a population as a whole, an estimate of the population through time is required.

There are a range of estimator techniques used in biology today for M-RC. They can essentially be grouped according to the number of samples taken (i.e. those that require 2, 3 or more captures). In a more complex manner they can also be grouped

according to the exact required outcome of the effect of a specific variable. Before choosing how to group data to use and which variables to consider as potentially influential, the four M-RC assumptions must be met, and a collection of sufficient M-RC data gathered to investigate different estimator techniques for use (Hayes & Steidl 1997; Thomas 1997; Reed & Blaustein 1997).

The data sets required for amphibian M-RC often comprise capture and recapture occasions in monthly or yearly sampling periods. These periods must have at least three sampling occasions to complete M-RC estimation. After the number of capture-recapture periods is sufficient, the next step used in model choice arrives from a decision as to whether a population is closed or open.

1.21.2 Closed and Open Populations; the Jolly-Seber Framework

Populations can be classified as either ‘open’ or ‘closed’. A closed population is defined as one that ‘remains unchanged over the period of study’ whereas an open population changes because of some combination of birth, death and emigration. Reviews of methods applicable to closed and open populations are given in White *et al.* (1982) and Pollock *et al.* (1990).

For more specific entrances to defined problems that population models have faced, papers by Cormack (1964), Otis *et al.* (1978), White *et al.* (1982), Seber (1986), Brownie (1987), Chao (1988), Huggins 1989, Pollock *et al.* (1990), Nichols (1992), Lebreton *et al.* (1992), Schwarz & Seber (1999) Pledger (2000), Brown (2001), Borchers *et al.* (2002), Schaub *et al.* (2004) and Link & Barker (2005) are more detailed.

A closed population implies that no individuals are deleted from or added to the population during the entire study period. Use of closed populations is generally accepted when this rule can be accepted and the likelihood of additions and subtractions to a population can be ignored (e.g. short time scale studies).

Two distinct advantages of a closed population model are;

- An improved estimation of population characteristics (due to a reduction in model parameters and variables considered).
- Relaxation of the assumption of equal catchability among individuals.

Generally, closed population models are less complicated in their assumptions but are highly specific to certain data types. Most are derivatives of the Cormack Jolly-Seber model (CJS) (Cormack 1964). The CJS method is applicable to almost any population estimation problem where it is possible to recapture and release a number of live amphibians on successive capture occasions. The occasions may occur within a single year or season, or, may be an annually recurring event (e.g. during a migratory return to a breeding pond).

The basis of the method is to examine every batch of captured amphibians for the presence of marked individuals and to classify all recaptured animals in accordance with their previous capture histories. Thus, an individual may be recaptured a number of times since the initial release event, or it may be recaptured only once, or not at all.

The following equations define the relevant components that would be identifiable in a typical CJS estimation problem;

$$a_i = \frac{M_i N_i}{N_i} \quad (i = 2, 3, \dots, l)$$

M_i = number of marked animals in the population.

a_i = proportion of marked animals in total population at time i .

N_i = total number of animals in the i^{th} sample.

$$\mathbf{M}_i = \frac{\mathbf{s}_i \mathbf{K}_i}{\mathbf{R}_i} + \mathbf{m}_i \quad (i = 2, 3, \dots, l-1)$$

$\mathbf{M}_i$ = number of marked animals in the population.

$\mathbf{l}$ = number of sampling events (this is the letter L).

$\mathbf{m}_i$ = number of marked animals in the i^{th} sample.

$\mathbf{s}_i$ = number released from the i^{th} sample after marking.

$\mathbf{R}_i$ = number of the s animals which are subsequently caught.

$\mathbf{K}_i$ = number of animals marked before time i which are not caught in the i^{th} sample, but are caught subsequently.

$$\mathbf{N}_i = \frac{\mathbf{M}_i \mathbf{n}_i}{\mathbf{M}_i} \quad (i = 2, 3, \dots, l-1)$$

$\mathbf{M}_i$ = number of marked animals in the population.

$\mathbf{n}_i$ = proportion of marked animals in total population at time i .

$\mathbf{N}_i$ = total number of animals in the i^{th} sample.

$$\hat{\mathbf{O}}_i = \frac{\mathbf{M}_{i+1}}{\mathbf{M}_i - \mathbf{m}_i + \mathbf{R}_i} \quad (i = 2, 3, \dots, l-2)$$

$\hat{\mathbf{O}}_i$ = population estimation based on closed assumption.

$\mathbf{M}_i$ = number of marked animals in the population.

$\mathbf{m}_i$ = number of marked animals in the i^{th} sample.

$\mathbf{R}_i$ = number of the s animals which are subsequently caught.

- The number of marked animals consists of the observed number captured, $\mathbf{R}_i$ plus the number not captured in i^{th} sample ($\mathbf{M}_i - \mathbf{m}_i$).

Immediately after time i there are two groups of marked animals. The $(M_i - m_i)$ and the s_i (from above equation $M_i = s_i K_i / R_i + m_i$) animals just released. Of the former group, K_i are subsequently caught; of the latter group, R_i are subsequently caught.

- Therefore, the ratio of K_i to the marked animals alive and free at time i would equal the ratio of the R_i to the marked animals just released, providing that the probability of recapture is the same for both groups. Now, the proportion of marked animals in the sample is taken to represent the proportion of marked animals in the population, hence:

$$N_i = \frac{M_i N_i}{m_i}$$

M_i = number of marked animals in the population.

n_i = proportion of marked animals in total population at time i .

N_i = total number of animals in the i^{th} sample.

CJS estimation of survival; from immediately after the i^{th} release to time $(i+1)$ is estimable by the ratio of marked animals alive at these times:

$$\hat{\phi}_i = \frac{M_{i+1}}{M_i - m_i + R_i}$$

$\hat{\phi}_i$ = population estimation based on closed assumption.

M_i = number of marked animals in the population.

m_i = number of marked animals in the i^{th} sample.

R_i = number of the s animals which are subsequently caught.

CJS estimation of immigration; is an estimate of the ‘dilution’ of the marked animals in the population. It is useful for determining recruitment from an adjacent population. The estimator of immigration (B_i) is:

$$B_i = N_i + 1 - \hat{\phi}_i (N_i - n_i + s_i) \quad (i = 2, 3, \dots, l-2)$$

B_i = estimator of immigration.

N_i = total number of animals in the i^{th} sample.

$\hat{\phi}_i$ = population estimation based on closed assumption.

n_i = proportion of marked animals in total population at time i .

s_i = number released from the i^{th} sample after marking.

Today, much of the current literature applying M-RC analysis to populations, studies the advances in a closed population M-RC framework (see Table 1.21.2). The most recent of these closed population theories addresses heterogeneity in capture probability to be modelled in a flexible framework (Huggins 1991; Amstrup *et al.* 2006). The conditional likelihood models of Huggins (1989) and Huggins (1991) allow capture probability to be modelled as a function of individual covariates (e.g. the distance from the point where an individual is detected to the nearest road may be a useful covariate as individuals that spend more time near roads are often more likely to be detected if the survey is conducted along them).

New finite-mixture models sharpen the results of wandering capture probabilities that can affect the continuity of results. They approximate individual heterogeneity in capture probability with unobservable group differences in capture probability (Norris & Pollock 1996; Pledger 2000). Examples for amphibians have proved vital in enhancing trends in site occupancy (e.g. Bailey *et al.* 2004; Schmidt 2005). Schaub *et al.* (2004) provides extensions to earlier CJS models providing a solution within a closed population estimator to the problem of temporary immigration at a site.

Table 1.21.2 Modern closed population methods (Amstrup *et al.* 2006).

Discrete-time models and associated estimation methods	
<i>Model</i>	<i>Approaches/methods</i>
M_{tbh}	<p>Estimating equation^a (Chao <i>et al.</i> 2001b)</p> <p>Generalized linear models using covariates^{a, b} (Huggins 1989, 1991)</p> <p>Conditional sample coverage (Lee 1996)</p> <p>MLE using mixture (Pledger 2000)</p> <p>(All approaches are valid for the submodels given below; some of them are not repeated in each model)</p>
M_{bh}	<p>Generalized removal^c (Otis <i>et al.</i> 1978)</p> <p>Jackknife^{a, c} (Pollock and Otto 1983)</p> <p>Sample coverage^a (Lee and Chao 1994)</p> <p>Estimating equation^a (Chao <i>et al.</i> 2001b)</p> <p>Nonparametric MLE (Norris and Pollock 1995, 1996b)</p>
M_{tb}	<p>MLE^{a, b, c} (Rexstad and Burnham 1991; Chao <i>et al.</i> 2000)</p> <p>Estimating equation or martingale method^a (Lloyd 1994; Chao <i>et al.</i> 2001b)</p> <p>Bayes approach (Lee and Chen 1998)</p> <p>Log-linear models (Cormack 1989)</p>
M_{th}	<p>Sample coverage^{a, c} (Lee and Chao 1994)</p> <p>Estimating equation^a (Chao <i>et al.</i> 2001b)</p> <p>Mixed logit models (Agresti 1994; Coull and Agresti 1999)</p> <p>Log-linear models or latent class models (Darroch <i>et al.</i> 1993; Agresti 1994)</p>
M_h	<p>Jackknife method^{a, c} (Burnham and Overton 1978)</p> <p>Moment estimator^c (Chao 1987)</p> <p>Sample coverage^a (Lee and Chao 1994)</p> <p>Estimating equation^a (Chao <i>et al.</i> 2001b)</p> <p>Martingale method (Lloyd and Yip 1991)</p> <p>Bootstrap estimator (Smith and van Belle 1984)</p> <p>Empirical Bayes approach (Huggins 2002)</p> <p>Nonparametric MLE (Norris and Pollock 1995, 1996b)</p>
M_b	<p>MLE^{a, b, c} (Zippin 1956)</p> <p>Estimating equation or martingale method^a (Lloyd 1994)</p> <p>Log-linear models (Cormack 1989)</p>
M_t	<p>MLE^{a, b, c} (Darroch 1958; Otis <i>et al.</i> 1978)</p> <p>Moment estimator^c (Chao 1989)</p> <p>Estimating equation or martingale method^a (Yip 1991)</p> <p>Binomial model (Schnabel 1938)</p> <p>Log-linear models (Fienberg 1972)</p> <p>Bayes and empirical Bayes (Castledine 1981; Smith 1988, 1991; George and Robert 1992)</p>
M_0	<p>MLE^{a, b, c} (Otis <i>et al.</i> 1978)</p> <p>(All estimators given above are valid here)</p>
<p>^a Available in software CARE-2. ^b Available in software MARK. ^c Available in software CAPTURE.</p>	

Link & Barker (2005) also provide a new model with improved robustness of results. However, despite the effectiveness of these new models that specifically address detailed assumptions relative to individual data sets, model-based estimation of individual capture result heterogeneity can still be sensitive to the choice of model form (Link 2004).

The most effective way to reduce this bias caused by individual capture result heterogeneity, while adding the fewest assumptions, is to sample a large portion of the population. Alternatively if such capture effort is not available it is useful to use an open population model that would compensate for variable result heterogeneity. Open population models are specifically designed for use when estimation of population characteristics is assumed to be open to additions (i.e. birth or immigration) and/or subtractions (i.e. deaths or emigration). Use of them enables a data set to be created that exhibits variable numbers of individuals over time. This situation in data is a particularly common phenomenon in seasonally migrating amphibians (Duellman & Trueb 1986).

The Open Jolly-Seber model (after Jolly 1965 and Seber 1965) is a fairly general technique and serves as a starting point for M-RC modelling (see White *et al.* 1982). The model allows year-specific estimates of apparent survival, capture probability (p), population size (N), and the number of new individuals entering the population (B). While population size can be estimated, it is often difficult to avoid some levels of bias in the estimation of this parameter set because of individual heterogeneity and other issues that allow for a combined level of variance to occur across a data range. The Open Jolly-Seber model is based upon a simple population growth model;

$$N(t+1) = N(t) * \text{phi}(t) + B(t)$$

$N(t)$ = the population size at sampling period t .

$\text{phi}(t)$ = the survival rate from t to $t+1$ for animals that were alive at occasion t .

$B(t)$ = the number of new animals added to the population by birth or immigration between t and $t+1$.

The main criticism of this model is that there is no direct observation of $N(t+1)$ and $N(t)$ but the model can estimate these quantities along with the parameters $\phi(t)$ and $B(t)$ with M-RC data. In doing so the model utilises samples from incomplete fractions of the population, dependent on the capture probability $p(t)$ at each occasion. This fraction is estimated using recaptures, whilst taking into account the fact that the population may be changing due to recruitment, mortality, or both.

The Open Jolly-Seber model assumes that samples are obtained instantaneously. In practice, this is not possible, so to ensure that the assumption is valid the samples should be completed over an interval that is short enough between capture periods. For example a study may be based on daily captures made over a one week period (secondary samples) with one year between the start of each capture period (primary samples). Pollock (1982) suggested that a useful design in this type of situation might be to consider the whole experiment as series of short-term population estimates.

What can also be achieved by having such a short timescale between M-RC sampling is a combination use of closed and open type models. Closed population models could be used to estimate N_i using the data from secondary samples which allow unequal catchability. The secondary capture data can then be pooled to form a data set for the primary capture periods and open population models used to estimate survival rate using these pooled data. This type of design has been tested and found to be more robust than the Jolly-Seber method. A full description of the design is given by Pollock (1982) and Pollock *et al.* (1990).

Over the years the basic Open Jolly-Seber model by Jolly (1965) and Seber (1965) has stood strong although is often criticised for its reliance on the following assumptions:

- Marked organisms are representative of the population of which inferences are to be made (i.e. marked organisms are a random sample of the population of interest).
- Numbers of releases are supposedly definitive.

- Marking is accurate, no tag loss, no misread tags, no data entry errors.
- All samples are made within relatively brief time periods (relative to time intervals between marking periods).
- The fate of individual organisms and the fates of organisms in differing cohorts are independent (counter example; banding of a mated pair of adult Canada geese; these might behave as one unit, instead of two independent individuals).
- Organisms in an identifiable class or group have the same survival and reporting probability (parameter homogeneity) for each time interval.
- Parameter estimates and sampling covariance is based on a good approximating model (i.e. the basis for inference is the model, thus, results are conditional on the model used).

The basic model design was subject to improvements by attempts to reduce fluctuations that occurred from survival rates and capture probabilities to create a 'Robust' design model (Pollock 1982; Pollock *et al.* 1990; Seber 1992; Schwarz & Arnason 1996; Schwarz & Seber 1999).

1.21.3 Closed and Open Populations; the Robust Pollock Matrix

The robust design by Pollock (1982) and Pollock *et al.* (1990) combines, in a single model, the advantages of both open and closed type population data sets. The advantages of using this are that there is more robust estimation of the parameters previously considered. This is achieved by estimation of certain parameters that were not otherwise estimable using either open or closed models when considered separately.

The advantages of this model are a direct consequence of the additional information provided by the short-term capture-history data. The technique can be considered to be a special case of using auxiliary data (see Pollock 2002). The original motivation behind designing the method derived from concerns about estimator robustness due to heterogeneity in capture probabilities. Some kinds of variation in capture probability, notably heterogeneity among individuals and permanent capture behaviour response,

could not be dealt with adequately in an open model setting. The survival estimators for the Pollock Open Jolly-Seber model are relatively robust to these sources of variation, whereas a straight abundance estimator used by a closed population would not be.

Mark-recapture models for closed populations deal primarily with capture response and heterogeneity in capture probabilities, leading to robust estimates of abundance under these conditions. Therefore combining the two reduces both capture response and survival estimator heterogeneity. The data structure using the Pollock method demands that periods of short-term sampling occurring over a survey design assume that the population is closed in the short term and open in the longer term, over which gains and losses are expected to occur. To perform this type of analysis a matrix of data has to be collated in a specific order. The data matrix in the robust design consists of presence and absence data through time. This is recorded by marking a score of '0' for no count and '1' for a positive capture. '1' occurs on the first capture occasion (i.e. when the animal is marked) and can also occur later as a recapture is made. Thus a capture history grid is formed;

For example;

Amphibian 1 101101

Amphibian 2 100000

Amphibian 3 100100

Amphibian 4 110111

In this example, Animal 1 was captured on the first day, not seen on the second day, recaptured on days 3 and 4, not seen on the 5th day and then recaptured on day 6. Animal 2 was captured on the first day and then never recaptured. If the example given above represents a single year of capture for each amphibian then multiple years would have to be recorded in primary and secondary sampling units. For example; primary sampling periods across 4 years (or secondary sampling periods) would correspond to a matrix with 20 capture histories. A row vector corresponding to a particular animal might consist of four groups of five capture values.

The first group of five numbers gives the capture history over the first year or primary period 1 (i.e. using the example below shows that the animal was captured on occasions 2, 3, and 5 of primary period 1). The second group of numbers indicates that the animal was not captured at all during primary period 2. In primary period 3 it was captured on the third secondary occasion, and in primary period 4 it was captured on secondary occasions 1, 3, 4, and 5.

Primary period	1	2	3	4
	01101	00000	00100	10111

To perform the analysis the matrix must consist of all capture history vectors for all animals caught at least once during the study. Pollock's matrix method is still in use today as it fits a wide range of perennially occurring organism surveys. Today there are also various methods that have further improved specific anomalies in the Open Jolly-Seber framework.

Gazey & Staley (1986) provided a sequential Bayes algorithm for estimating population size that was useful for when populations are small and recapture frequencies are low. Gelman *et al.* (1995) later provided a detailed discussion of general Bayesian approaches.

Most Bayesian likelihood approaches have been implemented in order to improve parameter estimation and avoid the problems that sometimes occur in classical methods (Ellison 2004b). Within the framework of open populations most Bayesian improvements have been restricted to resolving problems with survival rates by conditioning the first capture of an individual in a data set and thus sacrificing good estimates of abundance (Brooks *et al.* 2002).

In more recent Bayesian literature Markovian and Monte Carlo methods have been used with varying degrees of success to obtain inferences from likelihoods based on open populations (Dupuis 1995; Brooks *et al.* 2002). Other areas of improvement to the technique are the Horvitz-Thompson model (McDonald & Amstrup 2001) which estimates keys on the probability of capture at each trap occasion, and is therefore

quite general, and can be made a function of external covariates measured during a study.

O'Hara *et al.* (2002) recently provided critique of the technique and demonstrated methods of parameter estimation and prediction with simulated data. ter Braak & Etienne (2003) take the model further and apply it to a tree-frog metapopulation to demonstrate aspects of model uncertainty under pragmatic conditions.

1.22 Investigating Ecosystem Environmental Effects on Amphibian Populations

Wetlands are an integration of variable aquatic and terrestrial systems across a hydrological continuum (Euliss *et al.* 2004). Wetland flora and fauna are adapted to aquatic conditions and contribute to the ecological functioning of wetlands (Semlitsch 2006). Knowledge of aquatic ecological processes is well documented but studies of how they link with physical hydrologic processes are still largely in their infancy (Gregory *et al.* 1991; Bencala 1993; Naiman *et al.* 2000; Whittmann *et al.* 2004).

Despite previous studies on the interactions of amphibians, their environments and climate change, further work is still needed at local levels to better understand local functioning in order to identify conservation concerns and prescribe mitigation and management options (Collins & Storfer 2003; Root *et al.* 2003). Beyond information on species diversity, works are required that provide information on associations among species composition and local features, including environmental and biotic factors (Gottsberger & Gruber 2004). In turn, this may reveal community structure and function, which can be regulated through predictable environmental interactions of rain, hydroperiod, predation and competition (Semlitsch *et al.* 1996).

In general, little effort has been directed at determining how environmental and/or biotic conditions act on community structure and population in temporary or disturbed water bodies (Dixon & Heyer 1968; Heyer 1973; Gottsberger & Gruber 2004). To better understand this population data and environmental data can be correlated using multivariate analysis.

1.22.1 Using Multivariate Techniques

Multivariate techniques became widespread during the 1950s (James & McCulloch 1990) and have advanced greatly with the introduction of new statistical methods and faster computers to handle more complex analysis (Jongman 1995). Ecological surveys that have many species studied simultaneously, in relation to their environment, tend to be composed of large data sets organized in complex data matrices (Jager & Looman 1995).

Multivariate methods have a high summarising capacity, making analysis of these complex data sets possible (Leps & Šmilauer 2003). Interpretations can be made that are not possible with univariate statistics because several variables can be considered simultaneously (James & McCulloch 1990). This is accomplished by compressing multidimensional data in two directions simultaneously, reducing it to one or a few dimensions, or ‘low dimensional space’, which is comprehensible by the human mind (Gauch 1982; Palmer 1993). Typically, such representations detect the most important and interpretable measured environmental gradients (for example rainfall, hydroperiod and water chemical composition), while ignoring background noise or unexplained variation (Gauch 1982).

Multivariate methods in ecology can be divided into two broad categories; ‘gradient analysis or ordination’; and ‘cluster analysis or classification’ (Leps & Šmilauer 2003). The misapplication and interpretation of these multivariate methods is widespread and care must therefore be taken to apply suitable methods and recognize their limitations (James & McCulloch 1990).

1.22.2 Ordination Techniques

1.22.2.1 Ordination; Indirect and Direct Gradients

Ordination endeavours to represent sample and species relationships as faithfully as possible in a low-dimensional space (Gauch 1982). In determining which ordination methods to apply, the model of species response, followed by the type of gradient

analysis, needs to be examined. Two models of species response to environmental gradients are frequently used, ‘linear response’ and ‘unimodal response’.

The linear response is the simplest approximation, and works well over homogeneous data sets and therefore short gradients. In contrast, unimodal response works better over heterogeneous data sets and therefore wide environmental gradients, while assuming that species are optimized on the environmental gradient (ter Braak 1995).

Early studies of linear response demonstrated that its curves are too simple as an ecological response model and that unimodal models are more appropriate (ter Braak 1995). If no clear choice is intuitive, a simple test of gradient length, which measures diversity of a subject along the individual ‘gradients or ordination axes’ of the data set, will determine which response model is better to use (ter Braak 1995).

Within unimodal models there are two types of gradient analysis; ‘indirect gradient analysis/unconstrained ordination’, such as Correspondence Analysis (CA) or Detrended Correspondence Analysis (DCA); and ‘direct gradient analysis/constrained ordination’, such as Canonical Correspondence Analysis (CCA) or Detrended Canonical Correspondence Analysis (DCCA) (ter Braak 1995).

1.22.2.2 Using Indirect and Direct Gradient Analysis

Unconstrained ordination axes correspond to the direction of the ‘variability within the data set’ (Leps & Šmilauer 2003) and constrained ordination axes correspond to the directions of the data set variability that can be ‘explained by the environmental variables’ (Leps & Šmilauer 2003).

The dichotomy between indirect and direct gradient analysis is important (Gauch 1982; ter Braak & Prentice 1988). Indirect gradient analysis utilizes only the species by sample matrix. Essentially, environmental gradients are inferred from the species data and any environmental information is used only afterwards as an interpretative tool (Palmer 1993; Leps & Šmilauer 2003).

Direct gradient analysis, in contrast, utilizes external environmental data immediately in conjunction with species data and attempts to relate whether a species composition is related to a set of measured variables (Gauch 1982; Palmer 1993; Leps & Šmilauer 2003). Direct gradient analysis therefore allows a testable null hypothesis that species abundance is unrelated to measured variables (James & McCulloch 1990).

Some exploratory tests investigated the option of detrending unimodal methods (ter Braak 1995). This type of ordination should ideally be avoided when studying an estimate (as in a population) and fixed data (such environmental measurements). Detrending essentially corrects for the mathematical artefact known as ‘the arch effect characteristic of unimodal methods’ where their 2nd and higher order axes become distorted (an arched function of the first axis they are related to) (ter Braak 1995). This can happen in CA and CCA output graphs. This distortion, caused by unimodal distribution of species along gradients, can be prominent enough to impair the correct ecological interpretation of an output graph (Leps & Šmilauer 2003). Despite some advantages, detrending has come under criticism and although some criticisms have been rebutted successfully a number of problems still remain (Palmer 1993).

There are two basic approaches to detrending, first, by polynomials and secondly by segments (Hill & Gauch 1980). Detrending by segments lacks a convincing theoretical basis (Wartenberg *et al.* 1987; Knox 1989). Minchin (1987) also describes it as unstable in detrending. Pielou (1984) also warned that this method of detrending can sometimes lead to disruption of the underlying ecological data. Although detrending by polynomials is reputed to be more stable (ter Braak 1995), the technique is still debated by statisticians because removing the arch effect eliminates any naturally occurring arch, and can introduce other forms of distortion (Kenkel & Orloci 1986; Minchin 1987).

In the case of using CCA, Palmer (1993) argued that detrending is completely unnecessary as it does not produce an arch effect unless it occurs naturally. Therefore, performing a Detrended Canonical Correspondence Analysis (DCCA), unless for comparison with other detrended data, is inadvisable (Palmer 1993). Due to these differences in appropriateness of the various ordination gradient techniques, modelling analysis for population estimates against fixed data sets (e.g. in-situ

measurements) should be based on unimodal, direct gradient analysis. The choice method for this exploration of data can be achieved through CCA (Seaby *et al.* 2004).

1.22.3 Canonical Correspondence Analysis (CCA)

Correspondence analysis is an ‘exploratory data’ analytic technique designed to analyze simple two-way and multi-way tables that contain correspondence between the rows and columns. As opposed to traditional hypothesis testing designed to verify a priori hypotheses about relations between variables, ‘exploratory data’ analysis can be used to identify systematic relations between variables when there are no (or rather incomplete) a priori expectations as to the nature of those relations.

CCA (after ter Braak 1986; ter Braak 1994) is an ordination method in which the ordination of a biological matrix by correspondence analysis or reciprocal averaging is constrained by a multiple regression on the variables included in the environmental matrix. In ecological terms of population studies, this means that the ordination of species abundance estimates are constrained by their relationships to environmental variables. Thus this technique can aid interpretation of communities and environmental variables that shape them by identifying which environmental variables are determinants along the environmental gradients.

Alternative approaches to this type of analysis such as Correspondence Analysis (CA) or Principal Components Analysis (PCA), should not be used for data that contains estimates (such as population estimates) versus quantitative fixed data (such as rainfall measurements). This is because ordination techniques such as CA or PCA, which ordinate the abundance/population data, undertake an auxiliary analysis to identify and thus focus on quantitative environmental variables that may correlate with the ordination axes. This thus skews the interpretation of results by not comparing each individual data component impartially with every other component (ter Braak 1986; ter Braak 1994).

CCA differs from CA and PCA in that it excels at representing community data sets where species responses are unimodal (hump-shaped) and underlying environmental variables have been measured directly. The former can cause problems for methods

assuming linear response curves (i.e. PCA) but causes no problems for CCA (ter Braak 1986; ter Braak 1994). Underlying environmental variables that are measured from the environmental matrix can also constrain the ordination results in PCA, unlike any other ordination technique apart from CA. For this reason, CCA has been called a method for ‘direct gradient analysis’ (ter Braak 1986).

CCA is a robust test that combines positive aspects of indirect gradient ordination with aspects of regression (Leps & Šmilauer 2003). It allows for all axes, independent of each other, to select linear combinations of environmental variables, which maximize the dispersion of a species score (ter Braak 1986). CCA is therefore a constrained correspondence analysis in the sense that site scores are restricted to be a linear combination of measured environmental variables (ter Braak 1995). It is also completely unhampered by high correlations among species or environmental variables (ter Braak & Looman 1995). CCA is currently one of the most popular ordination techniques in community ecology. It is, however, full of anomalous trips for users due to its complexity. These dangers lie in several areas;

- It includes multiple regressions of community gradients on environmental variables. Therefore it is subject to all of the hazards of multiple regressions.
- Multicollinearity can be a problem. It is easy to believe that a relatively high coefficient, of multiple correlations, may imply a highly significant result, which it may not pragmatically.
- The method uses Linear Regression and therefore it is also likely that the response of the community to changes in an environmental variable may not be linear.
- As the number of environmental variables increases relative to the number of observations, the results become increasingly dubious as the appearance of very strong relationships becomes inevitable.
- Statistics indicating the ‘percentage of variance explained’ can be calculated in several ways, each for a different question, but users can confuse such statistics when reporting their results.

CCA does not explicitly calculate a distance matrix. But CCA, like CA and PCA, is based on the chi-squared distance measure where samples are weighted according to their totals (Minchin 1987). This gives high weight to species whose total abundance in the data matrix is low, thus exaggerating the distinctiveness of samples containing several rare or infrequently occurring species (Faith *et al.* 1987; Minchin 1987).

Since the statistical significance of a CCA analysis is determined by a randomization test, there is often no need to transform data to fulfill statistical assumptions. However, transformations can be used to dampen the influence of outliers. The choice of transformation impacts the location of sample scores, species scores, and environmental scores. A dampening transformation (e.g. a square root) tends to make samples and species more evenly spread out. Only rarely will transformation of environmental variables change the overall interpretation of an ordination (Roberts 1986).

1.22.4 Interpreting CCA Ordination

The solution of CCA is a graphical summary of data displayed as a two-dimensional ordination diagram that approximates the relationship between species and environmental variables (Figure 1.22.4). Species and nominal environmental variables, (which are non-quantitative in character but indicate exclusive classes to which individual observations belong) are represented as points. Quantitative environmental variables are displayed as arrows. When scaling of ordination diagrams is based on a biplot that focuses on inter-species distances, species are assumed to have an optimum position along each of the ordination axes with their abundances decreasing symmetrically in all directions from that point (ter Braak 1995). The length of the arrow or distance of the nominal variable from the centre of the origin indicates the importance of the environmental variable, while the direction indicates the environmental variable that is correlated with the species abundance (Figure 1.22.4).

Within such an ordination diagram, proximity implies similarity. Relative similarity or dissimilarity can be measured between points using chi-square distances.

Therefore, species abundance points in proximity share more similar correlations for environmental variables than species points far apart.

Figure 1.22.4 Diagrammatic example of a CCA biplot (Grant 2005).

Key: Canonical Correspondence Analysis (CCA). X represents species *Aeshna subpupillata*, *Agriocnemis falcifera falcifera*, *Anax speratus*, *Ceriagrion glabrum*, *Chlorolestes conspicuus*, *Elatoneura frenulata*, *Ischnura senegalensis*, *Nesciothemis farinosa*, *Orthetrum julia capicola*, *Paragomphus genei*, *Platycypha fitzsimonsi*, *Pseudagrion draconis*, *Trithemis arteriosa*, *Trithemis furva* and *Trithemis pluvialis*. Nominal variables are represented by (□), species are represented by (□). Zero denotes sites absent of species. Plant community type is represented by (+), with point 7 representing (1, 3, 5, 7, 11, and 14). For detailed description of plant communities and abbreviations of environmental variables see Appendix 10.0. For full species names see Appendix 11.0.

Likewise, environmental variables that are proximate to each other are predicted to have a large positive correlation, where as environmental variables pointing in opposite directions, have large negative correlations. Species abundance points projecting further from the origin of the coordinate system, in the direction of a particular environmental variable, are predicted to have a larger, more positive correlation with that environmental variable than species points that only project a short distance along the same environmental variable. Species abundance points projecting in the opposite direction of an environmental variable are predicted to be negatively correlated with that particular environmental variable.

Angles between objects (species points or environmental variables) that are less than 90 degrees, as measured from the origin of the coordinate system, projecting outwards, are predicted to be correlated. The greater the angle between objects in ordination space, the greater the predicted degree of uncorrelation and vice versa.

Testing the significance of the relation with environmental variables can be carried out by a Monte Carlo permutation test (Seaby *et al.* 2004). In this test, a null hypothesis is set up that states that the species composition is independent of the environmental variables and species distribution is simulated, thus obtaining an estimate of the distribution of the test statistic, F-ratio or eigenvalue. This test is also distribution free and does not depend on any assumption about the distribution of species (ter Braak 1995). Eigenvalues measure how much variation in the species data is explained by the ordination axis, thus values over 0.5 often denote a good separation of the species (ter Braak 1995).

1.23 Tropical Environments and Amphibian Population Dynamics

Arguably the greatest problem for biologists studying amphibian declines in the tropics is the lack of detailed information on natural localised fluctuations in species assemblages and the correct interpretation of the effects local environmental variables place on them (Pechmann & Wilbur 1994; Alford & Richards 1999; Young *et al.* 2001; Lips *et al.* 2005b). Tropical habitats vary enormously in altitude, seasonality, climate and environmental stability, making each geographic region or lifezone

different in its environment and population dynamics (Duellman 1990). Such variation is responsible for large differences in ecology, behaviour, abundance and diversity of amphibian lifecycles. This factor makes comparisons between sites and species difficult and may sometimes lead to presenting a false appearance of decline within populations (Skelly & Meir 1997; Alford & Richards 1997; Alford & Richards 1999; Marsh 2001; Schmidt 2003).

Species composition and/or species richness of tropical amphibian communities change over gradients in precipitation (Duellman 1988; Lee 1993), soil moisture (Friend & Cellier 1990), altitude (Lynch & Duellman 1980; Fauth *et al.* 1989), forest type (Crump 1971; Inger & Colwell 1977) and forest structure (Gascon 1991; Lieberman 1986; Urbina-Cardona *et al.* 2006), making comparisons between geographical regions difficult. Prey base and local habitat preferences have been suggested as influential (Janzen 1973; Toft 1980; Watling & Donnelly 2002; Beard *et al.* 2003). Although the mechanisms of these responses are unclear, amphibians' terrestrial and semi-terrestrial reproduction, moist/permeable skin and susceptibility to desiccation suggest immediate physiological limitations (Crump 1974; Duellman 1999; Wells 2007).

Historically, a larger proportion of herpetological research in the tropics has focused on those species that are aggregated at breeding sites, easier to locate, or more readily available within a habitat (McDiarmid 1994). Many temperate amphibians are easier to study because of the consistency of their annual breeding habits (Wells 2007). Such regulated phenology is determined by biological responses to seasonal climate change or the onset of late winter/early spring rains creating favourable breeding conditions (Beebe & Griffiths 2000). In contrast, relatively little is known of tropical amphibian movements outside of breeding sites or rates of exchange between populations. This is because so many tropical amphibians exist in complex metapopulations (Alford & Richards 1999; Young *et al.* 2001; Marsh 2001; Smith & Green 2005).

Amphibian metapopulations usually consist of a group of local populations inhabiting more or less discrete patches of habitat (Hanski 1998; Marsh 2001; Smith & Green 2005). They differ from collections of independent and subdivided populations in that there is substantial migration between local populations, so that no local population is

likely to remain closed or extinct for any length of time. However, where amphibians exist in small patches of specialist habitat (a common factor for tropical species) migration rates within a metapopulation can drastically affect rates of local population fluctuation (Nee *et al.* 1997; Marsh 2001; Leibold *et al.* 2004; Smith & Green 2005). When this occurs, even low rates of migration between local populations exhibit some degree of independence in their dynamics and place a population at risk of fragmenting and thus declining to extinction (Pounds & Crump 1994; Hanski 1997; Marsh 2001; Smith & Green 2005).

There has been substantial debate over the years regarding how ‘normal’ amphibian metapopulations change through time and whether they exhibit declines, but little theoretical work on this question (Pechmann *et al.* 1991; Pechmann & Wilbur 1994; Semlitsch *et al.* 1996; Marsh 2001; Smith & Green 2005), especially in the tropics (Young *et al.* 2001). Fluctuating amphibian metapopulations studied through time have been shown to be either increasing or decreasing over years and liable to swing in favour of abrupt short term successes with slower longer term decline trends (Pechmann & Wilbur 1994; Semlitsch *et al.* 1996; Alford & Richards 1999; Marsh 2001; Schmidt 2003). This type of population regulation would also operate differently depending on any stressors (Pechmann & Wilbur 1994; Semlitsch *et al.* 1996). Therefore, there is a considerable opportunity for bias if populations are declared to be declining on the basis of short term data. This creates a requirement for rigorous, repeatable and standardised annual data (Alford & Richards 1999; Marsh 2001; Schmidt 2003; Dodd & Dorazio 2004).

It is universally agreed that amphibian populations fluctuate considerably due to their variable annual recruitment patterns (Stebbins & Cohen 1995; Pough *et al.* 1998; Marsh 2001; Wells 2007) and that amphibian terrestrial life stages tend to be more constant in survival than egg, larvae and hatchling life stages (Wilbur 1980). However, due to the sheer diversity of lifecycle mechanisms and a distinct lack in ecological knowledge of tropical species, what is not known is what magnitude of population fluctuation indicates a successful survival trend and what physical and environment mechanisms act upon it (Alford & Richards 1999; Lips *et al.* 2005b). These anomalies make the requirement for multiple year studies of populations with identified correlation to stressors ever more urgent to address the correct estimation of

distributional change in amphibians (Blaustein *et al.* 1994b; Pechmann & Wilbur 1994; Marsh 2001; Schmidt 2003; Skelly *et al.* 2003; Dodd & Dorazio 2004; Smith & Green 2005).

1.24 Amphibian Decline at Caño Palma Biological Station

At Caño Palma declines in amphibian numbers and recognition of potential environmental stressors that may be involved had not previously been studied due to a lack of basic data on amphibian abundance in the area. This is a known and common problem in the tropics (1.16). This study is the first collation of quantitative amphibian population data for any amphibia at Caño Palma Biological Station. It was also the first study to quantitatively collect/analyse data on a selection of environmental stressors that may affect amphibian populations (see 1.6, 1.16 and 1.17).

The study comprised a mark-recapture style (1.21) collection and analysis of abundance data for 16 anuran amphibian species at Caño Palma. The study also collected data on local hydrology (1.6), climate (1.4) and water quality (by water chemistry analysis [1.17]). The population estimates generated from open population modelling (1.21) were combined with local hydrology, climate and water quality data to elucidate any correlations between amphibian population fluctuation and environmental stressors that may act as precursors to an amphibian decline (1.16).

The following objectives were derived from the study data to try to;

- 1) Estimate the abundance for 14 anuran amphibian species in Caño Palma's forest and 2 species within Caño Palma's grounds that are present before, during and after flooding events by presence and/or absence via mark-recapture methods (M-RC) and assess their relation to the rising water table.
- 2) Replicate (and compare) 3 years of data to strengthen the M-RC data, identify fluctuations in population size of the amphibian species over time.
- 3) Elucidate the movement and re-location patterns of amphibians before, during and after the annual flooding period.

- 4) Elucidate fluctuations in the local climate cycle and assess whether flooding events are part of the natural hydrological cycle of the area and/or a mechanism disrupting normal metapopulations of amphibians at Caño Palma.
- 5) Investigate fluctuations in the local climate cycle and determine any relationships between amphibian populations and the following climate variables: temperature, humidity, water table levels and water chemistry.
- 6) Document differences in the lifecycles of the species studied and describe ecological factors that may contribute to behaviour patterns for some of the species during periods of flooding.
- 7) Identify any disruptions to normal breeding behaviour of amphibia during environmental stress.

3.0 METHODOLOGY

To meet the objectives of this study (see 1.24) three experiments were devised. The experiments separated the core components of the study – environmental analysis, population and ecological study and correlation of affects, into sections to logically elucidate each objective.

Experiment 1 analysed environmental patterns at Caño Palma Biological station and provided data to elucidate objective 4 (1.24); *Elucidate fluctuations in the local climate cycle* and objective 5 (1.24); *Investigate fluctuations in the local climate cycle and determine any relationships between amphibian populations and climate variables.*

Experiment 2 analysed amphibian populations from mark-recapture data to elucidate objectives 1 (1.24); *Estimating abundance for 14 anuran amphibian species in Caño Palma's forest and 2 species within Caño Palma's grounds*, objective 2; *Replicate (and compare) 3 years of M-RC data to identify fluctuations in population sizes*, objective 3; *Elucidate movement and re-location patterns of amphibians*, objective 4; *Document differences in the lifecycles of the species studied*, and objective 5; *Identify any disruptions to normal breeding behaviour of amphibia during environmental stress.*

Experiment 3 analysed flooding, amphibian populations and water quality relationships to elucidate objective 4; *Elucidate fluctuations in the local climate cycle and assess whether flooding events are part of the natural hydrological cycle of the area and/or a mechanism disrupting normal metapopulations of amphibians at Caño Palma*, objective 6; *Document differences in the lifecycles of the species studied and describe ecological factors that may contribute to behaviour patterns for some of the species during periods of flooding*, objective 7; *Identify any disruptions to normal breeding behaviour of amphibia during environmental stress*, and parts of objectives 1, 2, 3 and 5.

3.1 Experiment 1; Investigation and Analysis of Environmental Patterns at Caño Palma

3.1.1 Summary of Experiment 1

This experiment investigated climate and hydrological cycles present at Caño Palma and whether any upstream pollution, or simple changes in water quality, occurred during periods of inundation. The experiment quantitatively gathered data for each factor at Caño Palma Biological Station to aid understanding the local river catchment of the Caño Palma canal. Daily notes on the wind speed, cloud cover, weather conditions, temperature, humidity, rainfall, water level and spring tidal movement were recorded at the Biological Station to build a profile of the climate.

The blackwater swamp pools in the Caño Palma area are known for their stable mineral composition (Myers 1990). Therefore water quality tests were used to inspect for potential differences in elements before, during and after a flooding event to detect any differences that may indicate a pollution episode. Direct measurements of water quality variables; pH, conductivity, iron, nitrogen, hardness, oxygen, carbon dioxide and salinity were collected through periods of inundation. The methods used to collect the data varied from electrical meter techniques to laboratory style titrations.

Data for water quality was collected every 2-3 days to monitor change through periods of flooding and normal hydrological cycle. Water quality data analysis was completed using statistical tests that questioned relationships between variables and sample years. Spearman Rank Correlation and Principal Component Analysis (PCA) were used to investigate the relationships. Multiple Analysis of Variance (MANOVA) was also used to check for inter-sample variation. Data was collated on a daily basis for the entire duration of surveys. Three series of results were completed; 2002-2003, 2003-2004 and 2004-2005 in the months October to February.

3.1.2 Detail of Climate Data Measurements

The climate variables collected during this study were temperature, humidity, wind speed, rainfall and water levels. A general weather log was kept daily noting

overnight rain, current rain, sunlight (by percentage cloud cover) and presence of wind as a reference to accompany the other variables.

Quadrats of cloud cover were replicated 3 times using a hand held quadrat. The quadrat tool used for collecting the results was a standard wire vegetation square (0.5 x 0.5 m). It was held up above the head of the surveyor and the percentage cloud estimated inside the quadrat. The 3 estimates were then pooled, creating an average that was recorded to the nearest 5%. Results for all of the variables, including cloud cover, were recorded in a single location within the grounds of Caño Palma Biological Station. To avoid observer bias, data was recorded by the author only.

Temperature was measured daily at the Biological Station in the morning (between 08:00-09:30) and in the afternoon (between 15:30-17:00). Temperatures were not recorded earlier than 08:00 as they were often at 23-24°C (similar to the nightly recorded minimum). Many morning temperatures in the local canal area did not stabilise until after 08:00, depending on cloud cover and solar radiation. Afternoon temperatures were not recorded past 17:00 due to falling temperatures toward sunset. Sunset passed between 18:00 and 18:30 regularly. Temperatures were also recorded within each forest transect, away from forest edge, to monitor the exact forest microclimates. This data was collected for comparison with the Biological Station measurements because temperatures can vary inside forest canopy and affect forest amphibian environments (Heyer *et al.* 1994; Chen *et al.* 1999; Burnham *et al.* 2001). A modern electrical water resistant temperature probe (Hanna Instruments™ HI 9064) was used to record temperatures. It was calibrated weekly against two Mercury filled Brannan™ max/min. thermometers that had been laboratory calibrated. The max/min. thermometers were located well above anticipated floodwater levels on the Biological Station grounds within a weather station box. Air temperatures that were measured using the electronic probe were recorded inside the weather box, adjacent to, and at the same time, as records taken for max/min. thermometers. This allowed simple comparison of the two results to check for equipment errors. Error with electrical equipment in tropical environments is a frequent problem due to increased levels of humidity (Heyer *et al.* 1994; Gunston 1998).

Humidity was measured as relative humidity (RH) immediately after temperature records (am & pm daily) using an electronic hygrometer (model Hanna Instruments™ HI 9065). The hygrometer was calibrated weekly for accuracy against a traditional whirling hygrometer (Casella Cel™ sling hygrometer). Rainfall was measured in millimetres fallen and recorded at the same time as temperature (am & pm daily). A manual emptying Canadian Environment AEST™ rain gauge (113mm circular gathering diameter) was used to collect rain and emptied after each reading. The rain gauge was located in a space, void of canopy cover, on the Biological Station grounds and above anticipated flood levels. The gauge was concealed in a protective capture cylinder, preventing spillage that could void a result.

An electronic anemometer was used to record wind currents in the Biological Station grounds. Wind speed was measured in miles per hour (mph) at the same time as temperature (am & pm daily). Calibration was performed in accordance with the manufacturer recommendation. Analysis of the results for the general climate data was completed using Kruskal Wallis and Mann-Whitney U-test statistics to reveal variance between years of results and to assist in calibration. Spearman Rank Correlation was used to investigate the flooding cycle by correlating rising water levels with precipitation and lunar cycles.

3.1.3 Hypothesis for Climate Data

The data analysis for the collated environmental results comprised the following;

- 1) Analysis and justification of suitable calibration to cope with potential environmental variances on equipment.
- 2) Analysis of the temperature and humidity.
- 3) Analysis of precipitation and water levels in the canal and how they correlated to rising water levels.

These three sets of results are discussed with respect to the following three questions;

- Are the environmental results of cloud cover, windspeed, temperature, humidity and rainfall consistent across the range of data and within years?

- Does temperature and humidity differ among years?
- Is there a correlation between spring tide water levels, and rainfall, and the occurrence of flooding?

To analyze question 1 the measurements taken with electronic equipment were tested for differences against mercury bulb equipment to monitor accuracy. The analysis used Kruskal Wallis Tests for non-parametric data and Analysis of Variance (ANOVA) for data that was normally distributed. The hypothesis tested was;

HYP 1-There is no significant difference/variation between electronic and traditional mercury bulb measurements.

To analyze question 2 Kruskal Wallis Tests for non-parametric data and Analysis of Variance (ANOVA) for data that was normally distributed were also used to investigate data further. The hypothesis formed for this analysis was;

HYP 2-There is no significant difference/variation between temperature and humidity when compared in all years.

To analyze question 3 Kruskal Wallis Tests, ANOVA and Linear Regression were used to summarise variance and investigate relationships between the variables of fluctuating water levels, rainfall, spring tides (moon cycle) and flooding. The hypothesis for this analysis was;

HYP 3-There is no significant difference between the variables of water level and rainfall between years.

All statistical analysis for the above hypotheses was completed using MINITAB™ Release 13 and 15 computer software.

3.1.4 Detail of Water Quality Measurements

Laboratory measurements of temperature, pH levels, carbon dioxide (CO₂), dissolved oxygen (DO), conductivity (mS), nitrogen (N), phosphorus (P) and hardness (DH)

(see 1.17) were performed to elucidate water quality in the Caño Palma canal. These elements were chosen for their broad spectrum importance in tropical aquatic environments and because they are known as precursors for pollution events (Hellawell 1986; Harrison 1992; Talling & Lemoalle 1998).

Samples of water were collected from the same in-situ area of the Caño Palma canal throughout the study. The canal samples were taken from directly opposite Caño Palma's boat dock (Figure 1.8.1) in the centre of the canal. A plastic water bucket dredge made from a 2 litre drinks bottle and a 30 cm diameter funnel attached to the neck was used to haul water samples from the canal. The bucket dredge had a 2.5 kg weight attached to its base and was thrown out into the canal, allowed to sink to the bottom, and pulled in on a rope line transversely crossing all depths of water from the centre line of the canal to the dock edge. Samples taken at the canal side were then transported immediately to the laboratory for analysis within 10 minutes.

Samples were transported with care and consideration, attempting not to agitate them and avoiding oxygenating the sample. Samples in the waterbottles were also filled to the very top of the sample bottle with no air bubbles, creating a seal that avoided agitation. Dissolved oxygen and hardness content were always analysed first as these can change over temperature gradients and over time if left for several hours (Hellawell 1986; Harrison 1992; Talling & Lemoalle 1998).

3.1.4.1 pH Levels

Levels of pH were recorded using a hand held wet bulb electrode meter (Hanna Instruments™ HI98128 pHep). The probe on the meter comprised a joint temperature and glass bulb electrode. The probe was immersed into a water sample so that both tips of the probes were covered in 10mm of sample. Water samples of approximately 50ml were used. The water samples were warmed to 25°C in a water bath to provide consistency across samples because electrodes can be subject to variable drift in results (Meredith 1974; Hughes 1993). The electrode probe was dipped into the water sample for 30 seconds or until the result reading settled still with no fluctuation. The result was then recorded.

A buffer solution of pH 7.0 was used to calibrate the meter. The buffer solution was rinsed with distilled water between samples to clean the electrode prior to use, thus avoiding contamination. If the sample was contaminated with organic contents (i.e. twigs or vegetation) it was strained using a 150 µm (micron) sieve to remove any debris that could have miss-aligned the probe. Calibration was conducted according to manufacturer instructions using pre-packaged manufacturer buffer solutions. Calibration required re-setting the electronic centre point of the electrode to pH 7.0 and pH 4.0. Two buffer solutions at pH 7.0 and pH 4.0 were used. The buffer solutions were used only once and were placed into a water bath to ensure accurate calibration at 25.0°C.

3.1.4.2 Conductivity (mS)

Conductivity was measured (in mS) using a combination dissolved oxygen (DO) meter with probe (Jenway™ Model 9071). The meter comprised a meter box, conductive metal rod and DO probe. The probe was immersed into a water sample so that both tips of the probes were covered in 20mm of sample. A water sample of approximately 50 ml was used. The water samples were warmed to 25°C in a water bath to provide consistency across samples. The probe was dipped into the water sample for 30 seconds or until the result reading settled still with no fluctuation. The result was then recorded.

3.1.4.3 Iron (Fe)

During preliminary tests for iron content, levels were found to be naturally low in Caño Palma canal (naturally low levels are usually those <5mg/l [Hellawell 1986]). To test for iron a simple indication of in-situ levels was all that was required as a signal of iron availability. Water absorbing iron test strips were used as an indicator. The strips used were made by Omega™ model WTS-480025. They were accurate to 0.01mg/l and sensitive for measuring from 0.02 to 5.0mg/l. The strips were dipped directly into water samples of 50ml and the colour change compared with a manufacturer provided colour scale. The water samples were warmed to 25°C in a water bath to provide consistency across samples. The technique required no mechanical reader or extra reagents.

3.1.4.4 Nitrate (N)

The method used in this experiment was a Colorimetric Chemical Analytical Method (CCAM 1969). 5.0ml of each water sample was placed in evaporating basins. 1ml of 1% urea was added and the basins were placed on a water bath at 100°C until the sample had completely evaporated. 1.0mol of hydrochloric acid was then added to the basins and the samples placed back into the water bath. The samples were then re-swirled (mixed) after 5 minutes and then left for a period of 10 minutes. 10ml of de-ionised water was then added to the samples and they were then left to cool to ambient temperature (between 20-25°C). Once at ambient temperature 15ml of 10% ammonia was added to the basins, and finally the sample analysed using a manufacturer nitrate 28 557-6 NHP colour comparison disc (CCAM 1969). The colour of the solution was compared with the disc sample colour range to find a match. The value was then read off of the scale and recorded as ml of nitrate.

3.1.4.5 Hardness (DH)

Hardness was measured by a simple titration method (Hanna Test Kits™) using a sodium hydroxide solution (NaOH in water), ethanol, ethylenediaminetetraacetic acid (EDTA) and calmagite indicator ($C_{17}H_{14}N_2O_5S$). A mixing bottle was filled to 23ml with a water sample and one drop of $C_{17}H_{14}N_2O_5S$ added to the sample. The NaOH solution was then added drop by drop to the sample. The bottle was swirled to mix after each drop was added until a light pink colour persisted. Each drop of the NaOH solution used to turn the colour end point equated to 1.25mg/l CO_2 .

3.1.4.6 Dissolved Oxygen (DO)

Dissolved oxygen was measured in-situ, or immediately into a dredged water sample, where possible using an electronic membrane probe (Jenway™ Model 9071). The probe was a polarographic oxygen electrode and is faster and more convenient to use than the standard Winkler DO analytical laboratory method. The electrode comprised of a rod with a thin oxygen permeable membrane stretched over it. Oxygen diffusing through the membrane was reduced by contact with the electrodes, generating a

current measured by the meter. Diffusion of oxygen through the membrane is proportional to the concentration at the surface of the membrane. Due to potential variation in electrical measurements from electrical drift the probe was calibrated against a Winklers titration kit (Hanna Test Kit™). The method involved the addition of manganese sulphate (MnSO₄), potassium hydroxide (KOH) and hydrogen sulphide (H₂SO₄) to a sample, followed by the titration using thiosulfate (S₂O₃²⁻).

To perform the procedure a mixture of KOH and MnSO₄ was added to a sample in a glass stopper bottle. The MnSO₄ reacts with KOH to form manganous hydroxide (Mn[OH]₂). In the bottle a brown precipitate signalled that there was dissolved oxygen in the sample. H₂SO₄ was then added to dissolve the precipitate to form manganic sulphate (Mn₂[SO₄]₃). The KOH added earlier then liberates iodine with the Mn₂(SO₄)₃, causing a brown colour. Iodine droplets were added and the number of moles of iodine equated to the number of moles of oxygen in the water sample. Four moles of S₂O₃²⁻ were titrated for each mole of oxygen, thus, 1.0ml of 0.025M sodium thiosulfate (Na₂S₂O₃) is equivalent to 0.025meq of oxygen. This value was multiplied by 8mg/meq to convert to mg O₂. When 200ml of original sample was titrated, 1.0ml 0.025M MnSO₄ equated to 1.0mg/l DO. This test can generally achieve a precision of 0.02mg/l DO. Temperature affected the concentrations of DO in water, with higher concentrations occurring at colder temperatures (Brown *et al.* 1997). To standardise DO tests a water bath was used to stabilise the reagents and water samples to 25°C.

3.1.4.7 Carbon Dioxide (CO₂)

Carbon dioxide was measured by a simple titration method (Hanna Test Kits™). The method used a mixture of ethylenediaminetetraacetic acid (EDTA), ethanol and phenolphthalein (C₂₀H₁₄O₄) in accordance with manufacturer's instructions. The technique neutralized CO₂ (as carbonic acid) in the water sample with a dilute sodium hydroxide solution to a pH of 8.3 using the C₂₀H₁₄O₄ indicator. This process converted carbonic acid to sodium bicarbonate. The reaction was:

5 ml of water sample was placed in a beaker. 1 drop of $C_{20}H_{14}O_4$ (pre-mixed in ethanol) was added to the sample. If the sample turned pink it was recorded as $<0.1\text{mg/l CO}_2$. If the solution remained colourless EDTA was added drop by drop using a 1.0ml syringe to the solution until it turned pink. The amount in ml was recorded and then multiplied by 100 to obtain mg/l CO_2 .

3.1.4.8 Salinity (ppt)

It has been traditional to express salinity not as percent, but as parts per thousand (ppt or ‰), which is approximately grams of salt per litre of solution. In other disciplines chemical analyses of solutions, and thus salinity, are reported in mg/l . This study used a titration method to detect sodium chloride (NaCl) concentrations reported in mg/l (Hanna Test Kit™). The salinity level in g/kg was determined by a mercuric nitrate ($\text{Hg}[\text{NO}_3]_2$) titration method. Using this test the pH is lowered to approximately pH 3.0 by addition of nitric acid (HNO_3). Mercuric ions react with chloride ions to form mercuric chloride (HgCl_2). When the excessive mercuric ions are present they complex with diphenylcarbazone ($C_{13}H_{12}N_4O$) to form a purple solution. The colour change from yellow to violet indicates the endpoint of the titration. The reaction was:

To perform the test a plastic test tube was loaded with 1ml of sample water. 1 drop of $C_{13}H_{12}N_4O$ was added to the sample. Whilst swirling (mixing) the solution HNO_3 was added drop by drop until the solution turned yellow. HgCl_2 was then added drop by drop from a graduated 1.0ml syringe until the solution turned violet. The ml of HgCl_2 used was read off of the syringe and multiplied by 40 to gain salinity in ppt.

3.1.5 Hypotheses for Water Quality

The data analysis for collated water quality results comprised an analysis and justification of calibration to realise potential environmental variances of equipment; an analysis of the temperature and humidity; and an analysis of precipitation and water levels and how they correlated to rising water levels. The analysis provided answers to the following questions;

- Are the water quality results consistent across data and between years?
- If there is a difference (above), how do the variables differ across years?
- Is there a correlation between variables and the occurrence of flooding?

To analyse question 1 measurements of variables were tested for differences using Kruskal Wallis Tests for non-parametric data and Multiple Analysis of Variance (MANOVA) for data that was normally distributed and to investigate data further. The hypothesis formed was;

HYP 1-There is no significant difference between water quality variables (pH, conductivity, iron, nitrogen, hardness, oxygen, carbon dioxide and salinity) and no variables fluctuated within and among years during the flooding event.

To analyse question 2, Spearman Rank Correlation was used to isolate differences and Principle Components Analysis (PCA) was used to further investigate the leading cause of variance between the variables. The hypothesis formed for this analysis was;

HYP 2-There is no significant difference or correlation between the water quality variables, water level and rainfall.

To analyse question 3 Spearman Rank Correlation was used to isolate differences between variables and Linear Regression was used to investigate any relationship between the data fluctuations. The hypothesis formed for this analysis was;

HYP 3-There is no significant correlations between water quality variables and water levels during the flooding event.

Statistical analysis for water quality was completed using MINITAB™ Release 13 and 15 computer software.

3.2 Experiment 2; Analysis of Amphibian Populations from Mark-Recapture Data

3.2.1 Summary of Experiment 2

Declines in amphibian numbers at Caño Palma are relatively unknown due to a lack of basic data on amphibian abundance in the area. The nearest data sets to include mark-recapture (M-RC) are from La Selva Biological Station near Puerto Viejo de Sarapiquí north of San Jose. This experiment provides the first quantitative abundance data for sixteen amphibian species at Caño Palma and stands as a baseline with which to compare future population data from around the Tortuguero area. To gain a fuller understanding of the population of amphibians at Caño Palma an initial understanding of the various habitats was required. It was recognised that Caño Palma comprised a *Manicaria* swamp forest with additional raised hammocks and glades (see 1.9 and 1.10). This patchy habitat was made more coherent by the occurrence of three vegetation zones within the – forest edge, occasional flooded, and *Manicaria*.

Each of the sixteen species considered in this study utilised one or more of these zones. In order to consider the differences in species habitat requirements in relation to population information gathered in each of these zones, residing species were split into forest environment species and pond residing species. At Caño Palma *Chaunus marinus* and *Rana vaillanti* were the only two species of anuran amphibian in this study that were deemed strictly pond breeding species as they mostly occurred around the Biological Station pond. The fourteen remaining species of anuran amphibian in this study were deemed forest dwelling species as they mostly occurred in deep *Manicaria* forest. Due to the diversity of trophic levels and biomes used by these forest species, combinations of survey techniques were used to locate species in their niches. The following survey techniques are sensitive methods that were deemed appropriate for use because they would net all of the species intended for survey, and involve realistic labour intensity for a solo surveyor operation;

- Visual Encounter Survey (Jaeger 1994; Crump & Scott 1994).
- Leaf-litter Quadrats (Jaeger & Inger 1994).

Surveys using these techniques were conducted on most days, both diurnally and nocturnally, within Caño Palma's forest environment for the fourteen forest dwelling anuran species, and around the Biological Station grounds for the two pond breeding anuran species.

This study analysed 3 sets of data over 4 months in 3 separate years in order to replicate 3 times the population levels of amphibians before, during, and after the flooding event to investigate the short and longer term knock-on effect to the population. The remaining 8 months of each year allowed natural emigration, immigration, birth and death to occur within all populations of each of the species studied.

The forest surveys were conducted along three designated linear transects within the forest (see Figure 1.9.1). All three transects were surveyed using visual encounter surveys (VES) and leaf-litter quadrats. The forest surveys consisted of walking one or two VES transects and completing a single leaf-litter quadrat per visit. Usually only one leaf-litter quadrat (either nocturnal or diurnal) was completed every two days, due to the long labour hours involved (up to three hours per quadrat). VES surveys were conducted between 08:00 and 11:00 for a diurnal survey with any quadrat performed after the transect walk, and between 20:00 and 01:00 for nocturnal surveys again, with a quadrat after a transect walk. Regular random non-survey days were assigned most weeks to ensure periodical rest for the forest, permitting undisturbed functioning for the forest ecosystem. These non-survey days also permitted surveyor recuperation, sorting of collected specimens and tidying of field information and equipment. During the 2002/03 season, there were 161 survey occasions from October to February, 2003/04 had 183 and 2004/05 had 243 surveys.

Caño Palma Biological Station grounds were surveyed in a random fashion, collecting all anurans from within the grounds and in the pond. Amphibians were not captured from edge vegetation around the grounds and were only treated as part of the grounds survey if they were physically present in the grounds. Animals were marked, released and recaptured within the grounds before, during and after a flood on a daily basis with the same recuperation days as per the forest survey. The Biological Station

grounds were treated as a single large quadrat. A total of 165 sampling occasions was completed for the M-RC of two resident species in and around the Biological Station grounds and pond.

Analysis of the results consisted of population estimates devised from Open Jolly-Seber population models using the program Simply-Tagging (Seaby *et al.* 2004), with additional calculations of Pollock's Robust Design matrix model. The population estimates were calculated through time to create graphs that would visually and statistically exhibit fluctuations in population abundance of amphibians in both the Biological Station grounds and forest. Using the Open Jolly-Seber with Pollock's Robust model refinements also allowed for natural recruitment and emigration.

3.2.2 Detail of Visual Encounter Surveys (VES)

Three 200m long transects 20m apart were constructed to collect VES data, thus covering a pooled area containing amphibians that spanned approximately 15000m² within the forest. Each transect was marked at 20m intervals to provide known points of origin in relation to habitat structure. The distance was designed in accordance with previous tropical studies (see Heyer *et al.* 1994; Doan 2003).

The 15000m² study site was realised to be of sufficient size to collect data whilst remaining practical with respect to the time constraints of solo surveyor effort. All three transects were located along the same linear start line proceeding north to provide three replicated transect lines (see Fig. 1.9.1). Only transect 3, which proceeded at a curved angle into Caño Palma's forest, required a modified non-linear route to avoid its terrain crossing areas that had previously been anthropogenically altered. The transect lines avoided regularly trodden access paths and were chosen to reflect a passage of change within the forest identified by the botanical investigation. Changes in botanical structure within the forest were chosen with prior knowledge that they contained different flora and amphibian species assemblages. All three transect lines bisected the same changes in botanical composition to provide standardised comparison of data between transects.

Each transect did not include forest edge because previous studies have shown that forest edge habitat can bias survey results in favour of edge species, causing comparison errors (Marsh & Pearman 1997; Tocher *et al.* 1997; Laurance *et al.* 1998; Schlaepfer & Gavin 2001; Fleishman *et al.* 2002; Toral *et al.* 2002; Parris 2004). Transect lines were cut to a maximum distance of 1.0m wide to ensure sufficient manoeuvrability for capture of animals and safe passage. Cuts of vegetation were sparse and kept to an absolute minimum to allow natural passage of animals through transects and to keep foliage intact for natural behaviour of amphibians within the study area to resume. Only the visual arena of the line transect was used for collecting, marking and identifying those amphibians that were within visual range. Pursuits off transects for capture were allowed if an amphibian left the visual arena. This technique gave a 1-2m visual zone either side of a line transect to search for amphibians. Transect walks were timed to ensure that they were equal in duration.

VES surveys in tropical environments are recommended to be conducted between 08:00 and 11:00 for a diurnal survey and between 20:00 and 01:00am for nocturnal surveys because this encompasses peak activity times for the majority of tropical anurans (Zimmerman 1991; Crump & Scott 1994; Graves 1999). The VES transects conducted in this survey took between 45-60 minutes per transect. Fifteen minutes flexibility was allowed for marking and identifications of amphibians.

3.2.3 Detail of Leaf-Litter Quadrats

The technique used in this study comprised the preparation of a series of small squares (quadrats) at randomly selected sites within a habitat and thoroughly searching those squares for amphibians by temporary removal of the leaf-litter layer. Random placement of quadrats was chosen for this study to isolate each quadrat as an independent sample and create equal opportunity for capture for amphibians. Random areas were generated using a romer grid placed over a map of Caño Palma's surveyed area. A random table of numbers was then used to select x and y grid locations from the romer grid.

10 x 10m quadrat areas were chosen as recommended by previous studies that also involved fewer than three field researchers conducting a sample (see Heyer *et al.*

1994). Quadrats were placed at random distances no more than 30m at right angles from one of the three VES transects. 30m was chosen to reflect a boundary for the survey and to limit captures to those animals occurring within the 15000m² of forest designated for the study. On occasion 10 x 8m or 8 x 8m quadrats were used with respect to practicality within the forest (i.e. fallen trees). The extra 2 x 1m or 2 x 2m of quadrat was then surveyed as close to the disturbance feature as possible. Quadrat sampling was performed 2-3 times per week and not daily due to its labour intensity. For this study quadrat surveys were conducted solely by the author, to reduce observer bias (see Jaeger & Inger 1994) and therefore a greater number of VES surveys were conducted than quadrat surveys. Obtaining a lower frequency of samples than those of VES is acceptable when these two methods are combined due to the different niche each technique samples (see Heyer *et al.* 1994).

3.2.4 Detail of Caño Palma Biological Station Survey

The survey boundary area for amphibians within Caño Palma Biological Station grounds was fixed in size and therefore was treated as a single large quadrat with the grounds to forest edge being the limit of the survey. The area was surveyed visually using the same technique for VES only in a non-linear fashion as the grounds were too small to warrant using a series of linear transects. Artificial and natural refugia occurring around the grounds were searched during survey in a similar fashion to quadrat sampling. The permanent pond in the centre of the ground was a natural focal centre of the search area and was surveyed both within and around its edge. Frogs were collected, marked and released at their site of capture around the grounds in the same manner as for forest specimens.

During inundation, techniques for survey were affected but remained standardised. VES transects continued normally but were acceptably slower due to wading in floodwater. Floating amphibians found by VES on transects were recorded as were those found clinging to vegetation at water level, those found on trunks, branches and leaves. Leaf-litter quadrats were kept random in their chosen location and dimensions remained 10 x 10m where appropriate. Instead of searching leaf-litter, *Raphia* and *Manicaria* palm axils within the 10 x 10m quadrats were counted and searched. Floating amphibians within a quadrat area were also recorded as were those found

clinging to vegetation at water level, those found on trunks, branches and leaves. During periods of heavy flooding it was occasionally necessary to survey vegetation by canoe due to terrain difficulties using the same speed and visual technique as for VES. When a capture for marking was required the canoe was exited and chest wading performed to engage in capture, identification and processing of an amphibian.

3.2.5 Detail of Mark-Recapture Technique

To study the fluctuations of metapopulations of amphibians before during and after flooding events a mark-recapture (M-RC) system was chosen to estimate the abundance of each species studied. To protect the amphibians during handling latex gloves were worn at all times during field work. Most species were captured in the hand. Some species such as *Rana vaillanti* and some *Leptodactylus* spp. were rapid leapers and had to be caught using a hand net. After individuals were identified, measured and marked they were released at the site of capture. If further identification was necessary individuals were placed in a plastic bag (to prevent loss of moisture) and transported back to the Biological Station where they were placed in a moist terrarium. Immediately after any further identification and processing the animal was then released at the site of capture. A bottle of clean rain water was carried during the study at all times and was used to rehydrate any frog or toad that may have become stressed from capture or study.

This study used toe-‘tipping’, a variant of toe-clipping. Amphibians were marked by removal of only the first or second phalanx of a toe as opposed to a whole digit. This method assists in toe re-growth and does not interfere with locomotion (Lüddecke & Amézquita 1999; Kinkead *et al.* 2006; Phillott *et al.* 2007). The toe-tipping rationale in this study was derived from Donnelly (1989a) and Donnelly *et al.* (1994) and minimised harm and identification errors by using only one clip per hand or foot. The clip codes used in this study continued numerically in an exponential pattern, and not randomly. Each individual frog therefore had an individual clip code. Due to the variety of different species studied, each incorporated the same coding pattern and thus no single frog possessed more than four digit tips removed, all of which were singular and on a different limb.

3.2.6 Detail of Population Modelling Approach

In consideration of the pragmatic features of the model and the survey data, the data was investigated using the Open Jolly-Seber technique with additional Pollock's Robust design matrix. This technique was chosen over modern multiple CJS covariate models because although the Open Jolly-Seber is arguably poorer at capture probability heterogeneity, the model can sacrifice this as variance, and place more emphasis on the arrival of population abundance results with consideration for between year emigration and death. This decision of variance choice of abundance over capture probability in the modelling procedure agrees with conclusions made by Schaub *et al.* (2004) who recommend that both qualitative and quantitative methods be used in model selection criterion. Schaub *et al.* (2004) also recommend that when temporary emigration is suspected, an open model be used. Pollock's matrix and combined model was used. Pollock *et al.* (1990) formula was:

$$X_{\omega}^i = \sum_{h=0}^{i-1} X_{\omega}^{kl}$$

X_{ω}^i = the number of animals from N_i that exhibit capture history $\omega \in \Omega$ over the i secondary periods of primary period i (where Ω is the set of all possible sequences of 0s and 1s over the i secondary periods);

X_{ω}^{kl} = the number of animals from m_{hi} that exhibit capture history $\omega \in \Omega$ over i secondary periods of primary i ;

X_{ω}^i = the total number of animals caught in primary period i that exhibit capture history ω over the i secondary periods; i) those previously captured at time $h = 0, 1, i - 1$, and; ii) those with secondary capture histories.

N_i = total number of animals in the i^{th} sample.

ω = denotes a transfinite ordinal. Ω = denotes total set of possible outcomes.

Most population estimates made from open population models with heavy assumption contain some results that are not fully compatible with the model and therefore need corrective methods, exclusion or consideration separately (Lebreton 1995). To analyse variation in abundance estimates between years separately an alternative population estimator was used, the Schnabel estimator. The Petersen-Schnabel closed population estimator is an extension of the Lincoln and Petersen basic population estimate (Seber 1982). The Lincoln and Petersen estimate is determined as;

$$N = \frac{M C}{R}$$

N = estimate of total population size.

M = total number of animals captured and marked on the first visit.

C = total number of animals captured on the second visit.

R = Number of animals captured on the first visit that were then recaptured on the second visit.

The Petersen-Schnabel estimate differs from the Lincoln and Petersen estimate in that it is applicable to a population count of samples taken over a multiple census over short time periods, when the population can be assumed to be constant in size (Seber 1982). The population estimate is a weighted average of a series of coupled Lincoln & Peterson estimates. For each sample (i), the following was determined;

$$N_i = \frac{\sum K_i n_i}{\sum s_i + 1}$$

n_i = Total number of individuals caught in the (i) sample

s_i = Number of individuals already marked (recaptures) when caught in sample (i)

K_i = Number of marked animals in the population just before the (i) sample is taken.

N_i is a function of recaptures and therefore precision of the estimate is increased by increasing total recaptures ($\sum s_i$). The assumptions of the Schnabel method are similar to the Lincoln and Petersen estimators but assumptions apply to all sampling periods (i.e. every individual in the population is assumed to have the same capture probability for a given sampling occasion, although capture probabilities can vary among sampling periods).

The sample year periods of 2002/03, 2003/04 and 2004/05 were considered separately and compared between different species but not between sample year periods to gain an additional understanding of the total population abundance of single sampling year periods. Mann-Whitney U-tests were applied to data to investigate the difference between years of population estimates. If data was shown to be normally distributed, an unstacked ANOVA was completed. To investigate data with other studies proportional abundance data was ranked and compared. This procedure involves crude creation of mean numbers per abundance counts of species and making them in order of highest abundance for comparison.

To compromise, and allow the forest to recuperate during each season of survey, fortnightly rest periods of 2 - 3 days duration were incorporated into the survey schedule thus allowing the forest some recovery to conditions of natural undisturbed activity. The three VES transects were alternated so that only a maximum of two were surveyed both diurnally and nocturnally on any single day.

No hypotheses were formulated for the M-RC population experiment because the investigation had no testable requirements.

3.3 Experiment 3; Investigation of Flooding, Amphibian Populations and Water Quality Relations

3.3.1 Summary of Experiment 3

This final experiment considered population data and investigated for signs of environmental correlation using multivariate analysis to understand how the

population of species at Caño Palma Biological Station and its forested land interacted with the local flooding.

To analyse the relationship between environmental data, water quality differences and population fluctuations in this study, Canonical Correspondence Analysis (CCA) was tested on all sixteen species of amphibian in the study to investigate variables and the probabilities of their influences. To perform CCA on complete data sets of abundance and environmental results, the CCA program 'Environmental Community Analysis' (ECOM) (Seaby *et al.* 2004) was used.

In ECOM population data was paired with each environmental variable according to the success or failure of a Pollock Open Jolly-Seber population abundance estimate. Therefore only specific population estimate days were tested against a successfully corresponding environmental variable.

The following environmental variables were modelled against Pollock Open Jolly-Seber population abundance estimates pH (*Env. 1*), conductivity (*Env. 2*), iron (*Env. 3*), nitrate (*Env. 4*), hardness (*Env. 5*), dissolved oxygen (*Env. 6*), carbon dioxide (*Env. 7*) and salinity (*Env. 8*). In a separate test the population estimates for each species were tested against water level data to investigate potential relationships of the flooding mechanism and populations. If levels of water quality were markedly different from normal fluctuating levels toxicity to amphibians could occur and this may affect population levels for some species (1.17).

3.3.2 Detail of Canonical Correspondence Analysis

For CCA to perform in this experiment it was necessary to transform data to achieve successful randomization and normal 'bell' shaped distribution of data (Palmer 1993). To successfully transform the environmental variables and Pollock Open Jolly-Seber population estimates for this study a natural Log $e(x + 1)$ was used. The transformation lowered the range of data without seriously compromising the data by causing bias. $x + 1$ was required as part of the Log to reduce error from especially low or high samples and frequent zero counts in the environmental variables.

To analyse the relationship between the CCA results a Kendal Rank Correlation was produced as part of the ECOM analysis output. Kendal Rank Correlation is a non-parametric correlation similar to Spearman Rank Correlation. Like other rank correlation methods the test produces a result 'T' which ranges from -1 through 0 to 1, indicating perfect negative correlation, no correlation and perfect positive correlation.

The advantage of a Kendall Rank Correlation over Spearman Rank Correlation and Pearson Correlation for use in CCA is that T can be used in partial correlation. Kendall's correlation was utilised to help descriptively explain differences in canonical axis relationships (Dytham 1999).

To isolate further any prominent or strong differences between variables, Linear Regression was used to interpret relationships between the data trends.

3.3.3 Hypotheses of Canonical Correspondence Analysis

The hypothesis formed for the CCA and its related analyses was;

HYP 1-The water quality variable data for pH, conductivity, iron, nitrate, hardness, oxygen, carbon dioxide and salinity exhibited no significant relationship with population fluctuations of the 16 amphibian species studied during the flooding event.

3.4 Collection of Voucher specimens

A voucher collection of specimens from the Caño Palma area was prepared for identification, genetic records and as a bank for future amphibian disease analysis (Appendix 2.0). The voucher collection was deposited in the herpetological collections at the University Costa Rica (UCR). Federico Bolaños of UCR verified species identification and assisted in preparing the samples.

Specimens were prepared in a traditional manner using guidelines by McDiarmid (1994). A weak 15% alcohol solution was used to kill amphibians. Additionally Lidocaine Hydrochloride (2% w/w), as Anbesol™ ulcer gel, was applied to the head area for larger and more active specimens that took longer than 30 seconds to

succumb to alcohol anaesthesia. Lidocaine is a derivative of Benzocaine which has successfully been used to euthanize amphibians for collecting purposes and is sometimes preferable for its sedating effects (Heyer *et al.* 1994; Brown *et al.* 2004; Cecala *et al.* 2007).

Once killed, amphibians were washed in clean, boiled water. A light, pH buffered, 10% formaldehyde solution was applied as fixative. Specimens with larger body cavities and developed limb muscles were injected with the solution. Samples were then stored in air tight plastic containers with clean cotton wrapping saturated in 10% formaldehyde. When the collection was completed it was transported to UCR where specimens were soaked in water and prepared for long term preservation in alcohol. Collection of amphibians was granted under license 030846321 supplied by the Ministerio de Recursos Naturales Energia y Minas (MINAE).

4.0 RESULTS

4.1 Experiment 1; Investigation and Analysis of Environmental Patterns at Caño Palma

The collection of climate and water quality data was successful for all field study seasons. The results for this section are presented in 4.1.1. Output graphs of the results can be found on pages 165-169 and 173-180. Raw data for this section can be found in appendix 3.0, 4.0 and 5.0. The climate data for the project commenced with the first field season (2002/03). Three field study seasons of data (November to February; 2002-2005) were analysed in detail. The data spans 72 days in 2002/03, 68 days in 2003/04 and 83 days in 2004/05 seasons. Differences in recording period were due to time available for collation of results, resources and surveyor effort.

4.1.1 Environment Data; Tests of Hypotheses

HYP 1-There is no significant difference/variation between electronic and traditional mercury bulb measurements. Hypothesis – accepted.

and;

HYP 2-There is no significant difference between temperature and humidity when compared in all years. Hypothesis – rejected.

Temperatures throughout all years of the study remained fairly stable from 22.0-31.0°C. A single occasion in 2002 was the highest recorded temperature at 35.4°C (Figure 4.4.1). Morning temperatures were generally higher than afternoon temperatures across all years (Table 4.1.1).

Table 4.1.1 Mean Electronic Morning Temperatures (EMT) and Mean Electronic Afternoon Temperatures (EAT) across years.

Year	EMT (Mean)	EAT (Mean)	N
2002/03	28	27.1	72
2003/04	26.9	26.3	68
2004/05	27.1	26	83
Mean	27.3	26.4	N/A

Temperatures across years were often mildly cooler during rainy periods, a feature typical of a lowland tropical wet rainforest climate (McGregor & Nieuwolt 1998; McDade *et al.* 1994) (Table 4.1.1).

Results between seasons of data varied although were stable within years (Figures 4.1.1-4.1.5). Electronic morning and afternoon temperature measurements between seasons was shown to be significantly different for both mornings (Kruskal Wallis, $H = 13.13$, $df = 2$, $P < 0.001$) and afternoons (Kruskal Wallis, $P < 0.001$, $df = 2$). Morning and afternoon temperatures were both graphically (Figure 4.1.1) and statistically different (Kruskal Wallis, $P < 0.001$, $df = 5$). One-way ANOVA suggested that temperature means varied between years but only slightly (ANOVA, $F = 11.47$, $df = 445$, $P < 0.001$).

Temperature measurements taken with electronic equipment were tested for differences against traditional mercury bulb equipment to monitor accuracy. Calibration of climate measuring equipment showed good consistency. Electronic morning (AM) temperatures calibrated against wet bulb thermometer morning temperatures exhibited good consistency with no significant differences (Mann-Whitney U-test, $P < 0.001$) within seasons. Electronic afternoon (PM) temperatures calibrated against the wet bulb thermometer afternoon temperatures also exhibited no significant differences (Mann-Whitney U-test, $P < 0.001$) for season 2003/04 and 2004/05 within seasons. However, season 2002/03 afternoon temperatures exhibited slight differences (Mann-Whitney U-test, $P = 0.649$) between wet bulb and electronic temperatures. One-way ANOVA showed an improved result within this difference (ANOVA, $F = 3.73$, $df = 1$, $P = 0.056$), but only slightly.

Humidity results had not historically been measured at Caño Palma Biological Station due to an absence of equipment. Humidity varied across years between 70 and 100% RH (Figure 4.1.2). Humidity measured at the Biological Station varied between years significantly (Kruskal Wallis, $P < 0.001$, $df = 5$) reflecting the varied levels in rain and water levels (Figure 4.1.2). Although humidity did not fluctuate greater than 60-100% RH, higher records were visually associated with increased rainfall during the wetter months of January, May, November and December a feature typical of lowland wet

tropical rainforest in Costa Rica climate (McGregor & Nieuwolt 1998; McDade *et al.* 1994).

Wind speed results were between 0.1-0.5 mph for all years. The results of wind speed measurements were not used in any specific analysis of the climate and environment because wind was often negligible within the forest and Biological Station grounds, even in high storms, due to the protection afforded by coastal forest and canopy cover. Wind speed was therefore not considered to affect amphibian populations or behaviour.

HYP 3-There is no significant difference between the variables of water level and rainfall between years. Hypothesis – rejected.

Rainfall occurred randomly but with a seasonal pattern. The heaviest rains almost always came late November to early December, which is concurrent with local knowledge (R. Ballard, P. B. C. Grant & D. Loth *pers. comm.*) and is also evident visually within the graphs. The heaviest rains (between 160.0 and 182.5mm) occurred more frequently overnight (ANOVA, $F = 29.33$, $df = 445$, $P < 0.001$). The mean rain levels for each season 2002/03-2004/05 varied significantly (ANOVA, $F = 4.23$, $df = 222$, $P < 0.05$) (Table 4.1.2), highlighting the varied pattern in rainfall for each season. Rainfall was highest in 2004/05 season peaking on four occasions between days 12-14, 51-52, 55-56 and 63-64 (Figures 4.1.3-4.1.5). On these four occasions major rainfall spikes discharged 227, 282.5, 332 and 302mm of rain over 24 hour periods. Across other years spikes in rainfall occurred just once in 2002/03 (sample day 11-12 [217mm]) and twice for 2003/04 (sample days 22 [189mm] and 45 [77mm]).

Table 4.1.2 Mean Rainfall and Total Rainfall across years.

Year	Mean Rainfall (MM)	Total Rainfall (MM)	N
2002/03	18	1302	72
2003/04	25.9	1767	68
2004/05	38.9	3230	83
Mean	27.6	2100	N/A

On Figures 4.1.3-4.1.5 water levels are shown in yellow. Although water levels do not have a corresponding axis they are placed on the graphs to show visual correlation between rainfall and water table saturation (flooding). On Figures 4.1.3-4.1.5 the corresponding water levels are labelled as Check M. The levels on the y axis represent the upper portion of measured water level that fluctuated in-situ in the canal. To gain the actual water depth figure of the canal 60cm is added to the figure from the y axis. Water levels were monitored constantly alongside other climate variables across all years. Water level in the Caño Palma canal was stable across sample years at a depth of 120-140cm, except where levels peaked from floods (Figures 4.1.3-4.1.5). Peak flooding levels were as high as 180cm-200cm in 2002/03 and 2003/04 respectively. In 2004/05 the later floods toward the end of the period were as high as 220cm canal depth, almost doubling the height of the canal.

There was a clear graphical relationship between rainfall and water levels (Figures 4.1.3-4.1.5). When the heaviest rains occurred the water table rose soon after (between 2 and 12 days [Figures 4.1.3-4.1.5]). Interestingly water levels showed no significant differences between seasons (ANOVA, $F = 6.41$, $df = 221$, $P < 0.002$) (Fishers = 1.971), but the 2003/04 and 2004/05 seasons showed some similarities (ANOVA, $F = 3.89$, $df = 138$, $P < 0.051$) (Fishers = 1.977). A positive correlation between precipitation and water levels was apparent within seasons for all seasons; 2002/03 Spearman Rank ($r = 0.154$), 2003/04 ($r = 0.192$), 2004/05 ($r = 0.307$).

Regression analysis was performed to investigate further the relationship between precipitation and water levels. Precipitation levels were found to be significantly different for all years; 2002/03 ($r^2 = 6.4\%$, $P < 0.001$ [X], $P = 0.031$ [Y]); 2003/04 ($r^2 = 4.5\%$, $P = < 0.001$ [X], $P = 0.082$ [Y]); 2004/05 ($r^2 = 7.6\%$, $P = < 0.001$ [X], $P = < 0.012$ [Y]) with influences on the X axes being the results clearly showing a relationship between increases in water levels and increased rainfall (see Appendix group 5.0 for analyses). This relationship is further investigated in 4.3 with population data for amphibians at Caño Palma Biological Station.

The moon cycle was included on Figures 4.1.3-4.1.5 to show when spring tides were at their fullest. There was no apparent relationship between high spring tides and the flooding events, although further work could reveal any relations in future.

Figure 4.1.1 Mean of morning (M-ET) and afternoon (A-ET) electronic temperatures (°C).

Figure 4.1.2 Mean% relative humidity (RH) recorded using electronic equipment.

Figure 4.1.3 2002/03 annual morning and afternoon precipitation (M-Prec. & A-Prec.) (mm); and water level fluctuation (Check) (mm). The moon cycle (presented as red circles) is for diagrammatic purposes only and has no quantitative value; point 100 = New Moon; point 120 = First Quarter; point 130 = Half Moon; point 140 = Full Moon.

Figure 4.1.4 2003/04 annual morning and afternoon precipitation (M-Prec. & A-Prec.) (mm); and water level fluctuation (Check) (mm). The moon cycle (presented as red circles) is for diagrammatic purposes only and has no quantitative value; point 100 = New Moon; point 120 = First Quarter; point 130 = Half Moon; point 140 = Full Moon.

Figure 4.1.5 2004/05 annual morning and afternoon precipitation (M-Prec. & A-Prec.) (mm); and water level fluctuation (Check) (mm). The moon cycle (presented as red circles) is for diagrammatic purposes only and has no quantitative value; point 100 = New Moon; point 120 = First Quarter; point 130 = Half Moon; point 140 = Full Moon.

Water quality data was recorded on contiguous occasions, usually every 2-3 days. Samples were gathered within the forest at randomised locations which included temporary, permanent, ephemeral and rainwater pools. The results were averaged and a mean of 3-4 samples for each variable recorded. In total 27 sample data sets (9 before, 6 during, and 12 post flood condition) were recorded for the 2002/03 survey season, 31 sample data sets (10 before, 7 during, and 14 post flood condition) were recorded for the 2003/04 survey season and 39 sample data sets (6 before, 8 during and 12 post flood condition, plus 13 during a secondary flood condition) were recorded for the 2004/05 survey season respectively (Appendix 4.1-4.3; Figures 4.1.6-4.1.11).

Results were collected for data analysis for all variables except nitrate which repeatedly resulted in negligible trace amounts or zero recordings. The remaining variables all showed quantifiable results and therefore were able to be tested according to the three hypotheses stated in the methodology (see Appendix group 5.0 for analyses). pH levels varied mostly between 5.7 and 7.5 across years (Figure 4.1.6). Conductivity varied between 0-0.8 mS (Figure 4.1.7). Hardness varied between 20-50 dHmg/l (Figure 4.1.8). Dissolved oxygen (DO) levels fluctuated between 2.0 and 10.0mg/l across all years with the highest level of just 12.5mg/l in 2004/05 (Figure 4.1.9). Peaks and troughs in DO levels could have been natural fluctuation as the levels were not especially great (Harrison 1992). Carbon dioxide levels fluctuated between 2.0-12.0mg/l with the highest reading being 18.8mg/l in 2002/03 (Figure 4.1.10). The high reading of 18.8mg/l is considered to be an anomaly result and its validity is uncertain. Peaks and troughs in carbon dioxide levels are fairly consistent with natural fluctuations (Harrison 1992). Salinity levels randomly fluctuated between 0 and 2.0ppt.

HYP 1-There is no significant difference between water quality variables (pH, conductivity, iron, nitrate, hardness, oxygen, carbon dioxide and salinity) and no variables fluctuated within and among years during the flooding event. Hypothesis – accepted.

and;

HYP 2 - There is no significant difference between the water quality variables, water level and rainfall. Hypothesis – accepted.

No sample results were normally distributed so non-parametric Kruskal Wallace Tests were performed to observe any differences between years within each variable. All variables showed only minimal significant differences between years (see Table 4.1.3). Although conductivity was variable among years the result was skewed by an outlier. Removal of the outlier (which was likely to be an anomaly result) resulted in no variation among years. However, it did return the data set to a normal distribution. Due to the presence of normal distribution a MANOVA test was then used to test for differences between variables and between years but focusing only on the normally distributed results. The MANOVA test resulted in no significant difference within conductivity and across years of conductivity (Appendix 5.3-5.5).

Table 4.1.3 Kruskal Wallace Test results for variation among years of water quality variables (showing significance at 95%).

Variable	H	df	P value	Observations
pH	28.66	2	<0.001	None
Cond	3.94	2	0.14	Skewed
Fe	14.31	2	<0.001	None
N	0	2	1	No Result
DH	51.41	2	<0.001	None
DO	8.44	2	0.015	None
CO ₂	9.85	2	0.007	None
SAL	9.23	2	0.01	None

To investigate the relationship between the variables further, and to see if any had specific relationships with each other, Spearman Rank Correlation tests were applied (see Appendix group 5.0 for analyses). The Spearman Rank Correlation tests revealed weak positive correlations in only 3 variables in 2 observations; salinity and conductivity, and, salinity and carbon dioxide. These factors were investigated further depth an explorative Principal Components Analysis (PCA) method. PCA is usually a parametric test but can be used for non-parametric exploration in such circumstances where the final result is not concerned with variances of all correlated factors (Dytham 1999).

HYP 3-There is no significant correlations between water quality variables and water levels during the flooding event.

Spearman Rank Correlation was used to isolate differences between variables and Linear Regression used to investigate further any relationship between variables in the data. The Spearman Rank Correlation test revealed only weak positive correlations within years with positive relationships only visible in pH, salinity, carbon dioxide, conductivity and iron. However, only significant results with $P < 0.05$ were found for salinity and water level in 2002/03 ($r = 0.523$) and pH and water level in 2004/05 data ($r = 0.408$). These two data sets were shown to have only slight relationships when analysed using Linear Regression. Outlier results skewed Linear Regression results in both sets causing poorer confidence, but, visually a slight positive trend was evident (see Figures 4.1.12 and 4.1.13).

Figure 4.1.6 pH levels of all sample year periods.

Figure 4.1.7 Conductivity levels of all sample year periods (mS/mho).

Figure 4.1.8 Hardness levels of all sample year periods (dHmg/l).

Figure 4.1.9 Oxygen levels of all sample year periods (mg/l).

Figure 4.1.10 Carbon dioxide levels of all sample year periods (mg/l).

Figure 4.1.11 Salinity levels of all sample year periods (ppt).

Figure 4.1.12 Regression plot of salinity and water levels for 2002/03 water quality data that successfully correlated by Spearman Rank Correlation.

Figure 4.1.13 Regression plot of pH and water levels for 2004/05 water quality data that successfully correlated by Spearman Rank Correlation.

4.2 Experiment 2-Analysis of Amphibian Populations from Mark-Recapture Data

The amphibian population data was split into two groups for separate analysis; Caño Palma Biological Station ground's pond data and Caño Palma forest data. Both sets of data received M-RC experimentation to test for abundance fluctuations before during and after floods using Pollock's Open Jolly-Seber population models. This allowed the analysis of count data through time and a full abundance estimate to be calculated through time.

4.2.1 Caño Palma Biological Station Pond Data

A total of 165 sampling occasions was completed for the M-RC of two resident species in and around the Biological Station grounds and pond; *Chaunus marinus* and *Rana vaillanti* (see Table 4.2.1 and 4.2.2). Nocturnal visual encounter surveys only were completed for the capture occasions as both species are only active during the night and are infrequently observed in the day (Savage 2002). A total of 579 *Chaunus marinus* and 496 *Rana vaillanti* were captured, marked and released. Recaptures were frequent in all years and both 2003/04 and 2004/05 exhibited inter-year recaptures. 'Animals caught N(i)' detailed in Tables 4.2.3 and 4.2.4 are only those that were captured by hand and do not include miss-captures (which were taken into consideration in Pollock Open Jolly-Seber analysis). Table 4.2.1 and 4.2.2 N(i) details the number of successful captures and recaptures by hand for both species. 'Marked animals in population' was calculated by taking the number of all individually recorded N(i) captured frogs or toads (which for 2002/03 would represent all of the clip coded animals as it was the first season) for that particular year and subtracting any inter-year recaptures (this would exclude year 2002/03). 'Newly caught animals' represents the number of newly caught individuals joining the population over the sampling period (again minus any inter-year recaptures).

The number of captures for *Chaunus marinus* and *Rana vaillanti* across years was fairly comprehensive (579 and 476 respectively, Table 4.2.1). Each season of count data for *Chaunus marinus* and *Rana vaillanti* varied between sample years significantly (Mann-Whitney U-test, $P < 0.05$).

Table 4.2.1 *Chaunus marinus* abundance data totals across years.

Year	2002/03	2003/04	2004/05	Total
N Sample occasions (i)	48	48	69	165
Number of captures N(i)	164	161	254	579
Marked captures in population	23	33	77	133
Newly caught animals	23	14	40	77

Table 4.2.2 *Rana vaillanti* abundance data totals across years.

Year	2002/03	2003/04	2004/05	Total
N Sample occasions (i)	48	48	69	165
Animals caught N(i)	84	169	243	496
Marked animals in population	26	31	33	90
Newly caught animals	26	25	32	83

Table 4.2.3 *Chaunus marinus* count data totals across years.

Year	N	Mean	Median	St. Dev.	S. E. Mean
2002/03	48	14.67	16	8.44	1.22
2003/04	48	15.13	16	11.66	1.68
2004/05	69	29.41	27	24.04	2.92

Table 4.2.4 *Rana vaillanti* count data totals across years.

Year	N	Mean	Median	St. Dev.	S. E. Mean
2002/03	47	6.76	0	10.77	1.57
2003/04	47	19.67	10	27.08	3.95
2004/05	69	28.19	12	62.59	7.59

For *Chaunus marinus*, the number of toads found decreased from 2002/03-2003/04 (164-161) but increased in 2004/05 to 254. For *Rana vaillanti* number steadily increased from 2002/03-2004/05 from 84-243 (see Table 4.2.1-4.2.2). However, there was no significant difference between 2002/03 and 2003/04 data for *C. marinus* (Mann-Whitney U-test, $P < 0.869$) nor between 2003/04 and 2002/05 data for *R. vaillanti* (Mann-Whitney U-test, $P < 0.835$). The data sets are limited in size with small total captures (579 for *C. marinus* and 496 for *R. vaillanti*) and low percentage recaptures (22.9% [133 recaptures from 579 captures] for *C. marinus* and 18.1% [90 recaptures from 496 captures] for *R. vaillanti*). The basic descriptive analyses are presented in Tables 4.2.1 and 4.2.2 respectively.

Examples of The Jolly-Seber results for each separate capture year season are presented in Figures 4.2.1-4.2.4 for *Chaunus marinus* and 4.2.5-4.2.8 for *Rana vaillanti* respectively. The recovery matrices for *C. marinus* and *R. vaillanti* that create the graphical results of Figures 4.2.1-4.2.8 are presented as tables in Appendix 12.0. The bars on each graph portray the estimated abundance through time using Open Jolly-Seber analysis with the Pollock *et al.* (1990) revised method. Y axis error bars show the error value of the population estimates and a linear trend line visually amplifies the projected average in abundance estimates over time. Example raw data from the computation of this analysis are presented in Appendix 6.1-6.5. Each capture year was treated separately for the initial Pollock Open Jolly-Seber analysis and did not regard inter-year recapture as different from yearly captures. The population estimates therefore reflect comparisons between sampling year period fluctuations. This helped to standardise each capture survey season for the purpose of unbiased comparison.

Population estimates were created successfully for all years of data for *Chaunus marinus* and *Rana vaillanti* (Figures 4.2.1-4.2.8). Population estimates for *C. marinus* varied between 12 and 33 in the first sample period of 2002/03 (Figure 4.2.1). The estimates were affected toward the latter end of the period (samples 36-47 [Figure 4.2.1]), possibly by lower recapture frequencies. Resident *C. marinus* were dominant throughout the sample period 2002/03 and new additions to the population were fairly infrequent occurring only on sample occasions 5-7, 11-13 and 27-33 out of 47 sample periods that had population estimate (Figure 4.2.2). In 2004/05 population estimates for *C. marinus* were more erratic with higher standard errors and several unsuccessful calculated estimates (Figure 4.2.3). This was possibly due to the higher flooding frequency that occurred in this sample year (4.1.1). This may have also disrupted dominance of territories in *C. marinus* and this is reflected in the increase in newly caught individuals through the sample period (Figure 4.2.4).

Population estimates for *Rana vaillanti* were not as successfully computed or complete as those of *Chaunus marinus* (Figures 4.2.5-4.2.8). This perhaps is reflected in the number of newly caught individuals that joined the population continually during all sample year periods (Figures 4.2.6 and 4.2.8). It is possible that *R. vaillanti*

had a higher recruitment level and lower territorial dominance among males at Caño Palma Biological Station's pond. Population estimates fluctuated at 5-50 in all sampling years (Figures 4.2.5 and 4.2.7). The highest estimate was 123 in 2004/05. However, this result is dubious and may have been a weak estimate in the model due to a very high standard error in survival estimate (116.1 – see Appendix 6.6).

An unstacked analysis of variance (ANOVA) test in MINITAB graphically showed the variance in abundance between years and demonstrated both variance of, and skewed distribution, in results for both *Chaunus marinus* and *Rana vaillanti* (Figures 4.2.9 and 4.2.10). Whilst this ANOVA test was technically flawed by being conducted on data that was not normally distributed, it graphically exhibited the mean data and variance in population abundance estimates through years. It also showed a number of outlier data points that may have been contributory to skewed or failed population estimates over sample year periods.

Figure 4.2.1 Population estimates of *Chaunus marinus* over sampling days for 2002/03; Pollock Open Jolly-Seber model.

Figure 4.2.2 Captures + capture additions of *Chaunus marinus* over sampling days for 2002/03; Pollock Open Jolly-Seber model.

Figure 4.2.3 Population estimates of *Chaunus marinus* over sampling days for 2004/05; Pollock Open Jolly-Seber model.

Figure 4.2.4 Captures + capture additions of *Chaunus marinus* over sampling days for 2004/05; Pollock Open Jolly-Seber model.

Figure 4.2.5 Population estimates of *Rana vaillanti* over sampling days for 2002/03; Pollock Open Jolly-Seber model.

Figure 4.2.6 Captures + capture additions of *Rana vaillanti* over sampling days for 2002/03; Pollock Open Jolly-Seber model.

Figure 4.2.7 Population estimates of *Rana vaillanti* over sampling days for 2003/04; Pollock Open Jolly-Seber model.

Figure 4.2.8 Captures + capture additions of *Rana vaillanti* over sampling days for 2003/04; Pollock Open Jolly-Seber model.

Figure 4.2.9 Graphical visualisation of variance in population estimates to show mean population levels for *Bufo (Chaunus) marinus* (* = outliers).

Figure 4.2.10 Graphical visualisation of variance in population estimates to show mean population levels for *Rana vaillanti* (* = outliers).

4.2.2 Caño Palma Forest Species Data

VES surveys, leaf-litter quadrat sampling and palm leaf-axil searching was performed before, during and after flooding events in all sampling year periods. During the 2002/03 season, there were 161 survey occasions from October to February, 2003/04 had 183 and 2004/05 had 243 surveys respectively (see Table 4.2.5). Survey occasions varied between years due to:

- Length of hydroperiod during flood - a longer hydro period ensured that the number of surveys required to equate to those collected pre-flooding had to be increased to ensure an unbiased result before, during and after comparisons.
- Number of floods - an increased frequency of flooding (as exhibited in 2004/05) ensured that the number of surveys required to be representative before, during and after comparison, had to be reduced.

A total of 586 sampling surveys were completed for the mark-recapture (M-RC) of the 16 species of forest dwelling anurans studied in this experiment (Table 4.2.5). This comprised 468 visual encounter transects (VES), 80 leaf-litter quadrats and 38 leaf-axil searches of the forest. The surveys yielded a range of total abundance for each species and showed which species were more frequently encountered across years and those species that were infrequently encountered and/or remained undetected during survey (Table 4.2.6).

Craugastor fitzingeri was found to be the most abundant frog by far in the forest with 290 individuals counted over all sample year periods. This was followed in order of decreasing abundance by *Oophaga pumilio*, *Craugastor polyptychus*, *Leptodactylus melanonotus*, *Bufo coniferus*, *Pristimantis diastema*, *Smilisca baudinii*, *Craugastor persimilis*, *Agalychnis callidryas*, *Scinax elaeochrous*, *Leptodactylus pentadactylus*, *Hypsiboas rufitellus*, *Dendropsophus phlebodes* and *Craugastor noblei*, respectively (see Figure 4.2.12 for totals). Some species increased in abundance through sampling years (e.g. *C. fitzingeri* – 61 [2002/03]; 107 [2003/04]; 122 [2004/05]), others fluctuated (e.g. *O. pumilio* – 55; 71; 64) and no species negatively declined through all three sampling periods (Table 4.2.6).

Two *Chaunus marinus* and two *Rana vaillanti* were discovered in each forest sample year period of count data. Numbers of each species recaptured (*Bufo coniferus*, *Oophaga pumilio*, *Craugastor fitzingeri*, *Craugastor polytychus* and *Leptodactylus melanonotus*) varied between years and between species significantly (Mann-Whitney U-test, $P < 0.15$ - $P < 0.81$) (Table 4.2.7 and 4.2.8). The high Mann-Whitney U-test ‘P’ values also suggested there was a lack of quantitative population abundance results when compared with failures or abundance estimate values of zero (0) by the Pollock Open Jolly-Seber model test.

An unstacked ANOVA test was performed for each forest species between sampling years to test for variability (as per the statistical testing for *Chaunus marinus* and *Rana vaillanti* in the Biological Station pond). Each ANOVA test failed to exhibit significant differences indicated by $P > 0.05$ (e.g. $P = 0.085$ for *Oophaga pumilio*). This factor was confirmed by viewing skewed histogram results for unstacked ANOVA tests for *O. pumilio* over all years (e.g. Figure 4.2.13). Not all species were able to be adequately computed by Pollock Robust design or Open Jolly-Seber estimation. Those that did often had gaps and anomalies within results (Figures 4.2.14-4.2.16).

Table 4.2.5 Summary of survey effort for forest amphibian species through sampling years. Dir = Diurnal, Noc = Nocturnal, VES = Visual Encounter Survey, LLQ = Leaf-litter Quadrat, LLA = Leaf-litter Tree Axil Plot.

Sampling Year	Dir VES	Noc VES	Dir LLQ	Noc LLQ	Dir LLA	Noc LLA	Totals
2002/03	62	61	16	12	5	4	160
2003/04	77	82	11	8	2	3	183
2004/05	95	91	17	16	14	10	243
Totals	234	234	44	36	21	17	586

When totals were compared with Scott (1976) data for La Selva Biological Station (the nearest known available data set to the study site), they exhibited similar totals in abundance for some species (e.g. *Craugastor noblei*) but different totals in abundance for the remaining species (Table 4.2.6). Not all forest dwelling species could be

compared with Scott (1976) because of differences in species assemblages. Where species assemblages differed, a similar species of the same genera that would have filled the same niche habitat was chosen. This allowed a more general, but nonetheless still accurate, representation of the abundance of species within both Caño Palma's and La Selva's forest. *Bufo coniferus*, *Oophaga pumilio*, *Craugastor noblei*, *Craugastor persimilis*, *Craugastor polyptychus*, *Pristimantis diastema* and *Rana vaillanti* were used from Caño Palma and *Bufo haematiticus*, *Oophaga pumilio*, *Craugastor noblei*, *Eleutherodactylus bransfordi*, *Eleutherodactylus biporcatus*, *Pristimantis diastema* and *Rana warschewitschii* were used from La Selva (Scott 1976).

Figure 4.2.11a and 4.2.11b Total abundance (Ni) forest data for forest amphibian species at Caño Palma and from La Selva (Scott (1976)).

Table 4.2.6 Complete abundance (Ni) forest data for forest amphibian species through sampling years (includes inter-year recaptures for each sampling year).

Species	02./03	03./04	04./05	Totals	Totals (Scott 1976)
<i>Bufo coniferus</i>	20	22	69	111	4^a
<i>Chaunus marinus</i>	0	1	1	2	n/a
<i>Oophaga pumilio</i>	55	71	64	190	32
<i>Agalychnis callidryas</i>	10	14	6	30	n/a
<i>Dendropsophus phlebodes</i>	1	3	0	4	n/a
<i>Hypsiboas rufitelus</i>	1	2	2	5	n/a
<i>Scinax elaeochrous</i>	7	15	1	23	n/a
<i>Smilisca baudinii</i>	12	15	9	36	n/a
<i>Craugastor fitzingeri</i>	61	107	122	290	n/a
<i>Craugastor noblei</i>	0	2	1	3	3
<i>Craugastor persimilis</i>	10	9	15	34	9^b
<i>Craugastor polyptychus</i>	45	40	58	143	70^c
<i>Leptodactylus melanonotus</i>	50	39	46	135	n/a
<i>Leptodactylus pentadactylus</i>	5	10	2	17	n/a
<i>Pristimantis diastema</i>	9	38	43	90	12
<i>Rana vaillanti</i>	0	2	0	2	5^d

- a) Nearest comparable species for Scott (1976) was *Bufo haematiticus*. Species would fill niche of *Bufo coniferus*.
- b) Nearest comparable species for Scott (1976) was *Eleutherodactylus biporcatus*. Species would fill niche of *Craugastor persimilis*.
- c) Nearest comparable species for Scott (1976) was *Eleutherodactylus bransfordi*. Species would fill niche of *Craugastor polyptychus*.
- d) Nearest comparable species for Scott (1976) was *Rana waschewitschii*. Species would fill niche of *Rana vaillanti*.

Table 4.2.7 Numbers of newly marked (Mi) and unmarked but sighted/miss-captured (mi) forest amphibians through sampling years.

Species	02./03		03./04		04./05		Totals
	Mi	mi	Mi	mi	Mi	mi	Mi + mi
<i>Bufo coniferus</i>	14	6	14	8	36	33	111
<i>Chaunus marinus</i>	0	0	1	0	1	0	2
<i>Oophaga pumilio</i>	44	11	52	19	52	12	190
<i>Agalychnis callidryas</i>	9	1	12	2	6	0	30
<i>Dendropsophus phlebodes</i>	1	0	3	0	0	0	4
<i>Hypsiboas rufitelus</i>	1	0	0	2	2	0	5
<i>Scinax elaeochrous</i>	6	1	10	5	1	0	23
<i>Smilisca baudinii</i>	9	3	9	6	6	3	36
<i>Craugastor fitzingeri</i>	32	29	63	44	85	37	290
<i>Craugastor noblei</i>	0	0	2	0	1	0	3
<i>Craugastor persimilis</i>	9	1	8	1	13	2	34
<i>Craugastor polyptychus</i>	22	23	18	22	36	22	143
<i>Leptodactylus melanonotus</i>	28	22	11	28	28	18	135
<i>Leptodactylus pentadactylus</i>	5	0	8	2	2	0	17
<i>Pristimantis diastema</i>	9	0	25	13	40	3	90
<i>Rana vaillanti</i>	0	0	1	0	0	0	1

Table 4.2.8 Numbers of recaptured (Ni) and inter-year (intNi) recaptured forest amphibians through sampling years.

Species	02./03		03./04		04./05		Totals
	Ni	intNi	Ni	intNi	Ni	intNi	Σ Ni
<i>Bufo coniferus</i>	1	0	1	1	10	1	14
<i>Chaunus marinus</i>	0	0	0	0	0	0	0
<i>Oophaga pumilio</i>	10	0	11	6	14	8	49
<i>Agalychnis callidryas</i>	0	0	0	0	0	0	0
<i>Dendropsophus phlebodes</i>	0	0	0	0	0	0	0
<i>Hypsiboas rufitelus</i>	0	0	0	0	0	0	0
<i>Scinax elaeochrous</i>	0	0	0	0	0	0	0
<i>Smilisca baudinii</i>	0	0	0	0	0	0	0
<i>Craugastor fitzingeri</i>	4	0	6	0	7	2	19
<i>Craugastor noblei</i>	0	0	0	0	0	0	0
<i>Craugastor persimilis</i>	0	0	0	0	0	0	0
<i>Craugastor polyptychus</i>	4	0	1	2	0	0	7
<i>Leptodactylus melanonotus</i>	7	0	1	1	1	1	11
<i>Leptodactylus pentadactylus</i>	1	0	0	0	0	1	2
<i>Pristimantis diastema</i>	0	0	0	0	1	0	1
<i>Rana vaillanti</i>	0	0	1	0	0	0	1

Figure 4.2.12 The percentage composition of species across sampling years (2002/03, 2003/04 and 2004/05).

Figure 4.2.13 Graph showing skewed distribution population estimates that failed to adequately determine a strong mean in data for *Oophaga pumilio*.

Figure 4.2.14 Population estimates of *O. pumilio* over sampling days for 2003/04; using Pollock Open Jolly-Seber model.

Figure 4.2.15 Captures + capture additions of *O. pumilio* over sampling days for 2003/04; using Pollock Open Jolly-Seber model.

Figure 4.2.16 Captures + capture additions of *Leptodactylus melanonotus* over sampling days for 2003/04; Pollock Open Jolly-Seber model.

Figure 4.2.17 Proportional Abundance of Caño Palma and La Selva Biological Station Compared Total Populations.

Petersen-Schnabel estimators were used where results from Open Jolly-Seber population estimators performed poorly or where only a handful of population estimates were computed. The results and comparisons of the successful Pollock Open Jolly-Seber and Petersen-Schnabel estimators for forest amphibian populations are presented in Tables 4.2.9. Table 4.2.10 shows the more thorough population estimate achieved over simple count data for a range of the species studied.

Table 4.2.9 Pollock Open Jolly-Seber population estimates (JS) from best estimates and indicative Peterson-Schnabel estimates (PS) for forest amphibians that were recaptured through sampling years. ‘~’ indicates failure of model test; SE = standard error.

Species	Sample Year Period											
	02./03				03./04				04./05			
	JS	SE	PS	SE	JS	SE	PS	SE	JS	SE	PS	SE
<i>B. coniferus</i>	~	~	148	124	~	~	191	122.5	18	12	239	62.4
<i>O. pumilio</i>	30	31.2	146	33.9	15	10.9	148	20.47	15	0	121	14.6
<i>C. fitzingeri</i>	~	~	477	225.6	~	~	819	264.8	78	10.5	773	224.5
<i>C. polyptychus</i>	~	~	246	111.1	~	~	298	159.6	2	10	~	~
<i>L. melanonotus</i>	12	9.6	201	69.6	57.3	32.3	~	~	4	0	385	203.7

Table 4.2.10 Complete abundance data (Ni) compared against Peterson-Schnabel estimates (PS) for forest amphibians that were recaptured through sampling years. ‘~’ indicates failure of model test.

Species	Sample Year Period					
	2002/03		2003/04		2004/05	
	Ni	PS	Ni	PS	Ni	PS
<i>B. coniferus</i>	20	148	22	191	69	239
<i>O. pumilio</i>	55	146	71	148	64	121
<i>C. fitzingeri</i>	61	477	107	819	122	773
<i>C. polyptychus</i>	45	246	40	298	58	~
<i>L. melanonotus</i>	50	201	39	~	46	385

Petersen-Schnabel estimates for *Oophaga pumilio* clearly show higher estimates than that of Open Jolly-Seber population estimates across all years (e.g. JS = 30 and PS 146 in 2003/04). This difference is largely because the Petersen-Schnabel is a closed estimate of the total population at a fixed point whereas the Open Jolly-Seber is an estimate of the population of frogs present at the time of survey. The Petersen-Schnabel estimates do, however, show similarities in dominance of species with the highest estimates. For example, *Craugastor fitzingeri* exhibited an Open Jolly-Seber result of 78 in 2004/05 sample year period and a Petersen-Schnabel estimate result of 773, both of which are higher than their corresponding, comparative tabled species.

4.3 Experiment 3-Investigation of Flooding, Amphibian Populations and Water Quality Relationships

HYP 1-The water quality variable data for pH, conductivity, iron, nitrate, hardness, oxygen, carbon dioxide and salinity exhibited no significant relationship with population fluctuations of the 16 amphibian species studied during the flooding event.

To analyse hypothesis 1 (HYP 1) certain assumptions and data set requirements were not able to be met. Kendall Rank Correlation and CCA was intended to be used to isolate differences between variables and Linear Regression intended to be used to investigate any cause and affect between the variable within data that fluctuated. This hypothesis was only possible for some of the environmental variables and some of the population data sets studied.

All species except *Chaunus marinus* and *Rana vaillanti* failed the criterion for CCA testing due to limited successful population estimate output. Even species such as *Oophaga pumilio* and *Craugastor fitzingeri* that had significant abundance count data and a handful of recapture results failed to give substantial Pollock Open Jolly-Seber population estimate results that would have enabled successful comparison with environmental data over the before, during and after flooding periods. Due to the continual population estimate success across the before, during and after flood timing periods by *Chaunus marinus* and *Rana vaillanti* some analysis on all environmental variables except iron and nitrogen was accepted for these two species. The hypothesis formed for this analysis (HYP 1) was therefore altered to HYP 1a;

HYP 1a-The flood water level data and water quality variable data for pH, conductivity, hardness, dissolved oxygen, carbon dioxide and salinity exhibited no significant signs of a relation with population data for *Rana vaillanti* and *Chaunus marinus* during the flooding event – hypothesis rejected.

CCA for *Chaunus marinus* and *Rana vaillanti* was successfully computed for water flooding levels and water quality variables (except iron and nitrogen) (Figures 4.3.1-4.3.4). Multicollinearity was successful for all years of analysis ($R < 0.05$, $VIF < 1.5$) (see Appendix 7.0 and 8.0 for examples of raw computation). The CCA analysis of

flooding levels showed a negative trend in all years for *Chaunus marinus* but one that was highly associated with the flooding cycle (e.g. Figure 4.3.4). From the population abundance data it was visibly clear that the flooding caused a break in population estimates from a lack of calculations performed by the model and this is amplified strongly in the CCA result. For *Rana vaillanti* the population data exhibited too many blank zero counts to be of any qualitative use for interpretation by the CCA. However, the population data did show a similar graphical output as *C. marinus* when computed with further successful population abundance estimates.

The relationship between water flooding levels and population abundance data for *Chaunus marinus* was further investigated by use of Linear Regression for all sample year periods. The Kendall Rank Correlation showed good positive relations between the variables ($r^2 = 0.57-0.23$). Linear Regression output for all years of flooding associated with population abundance for *C. marinus* exhibited positive association ($r = 0.28$, $P = 0.38$ [2002/03], $r = 0.43$, $P = 0.068$ [2003/04], $r = 0.062$, $P = 0.76$ [2004/05]) but not always with significant probability (Figures 4.3.5 and 4.3.6). The presence of outliers may have skewed results in sample year periods 2002/03 and 2004/05. Removal of these outliers subsequently improved results and improved confidence in results for 2002/03 and 2004/05 data sets ($r = 0.43$, $P = 0.22$ [2002/03], $r = 0.12$, $P = 0.61$ [2004/05]) but with similar conclusion that population abundance estimates were related to rises and falls in water levels.

Altered behaviour/response to flooding by amphibians during the flood included a range of different changes including:

- 1) Reduction in breeding activity/lack of male calling.
- 2) Alteration in physical location in the forest (displacement from original territory).
- 3) Climbing and swimming to avoid the flood water.
- 4) Aggregation of frogs in leaf-axils of *Raphia* spp. and *Manicaria* spp. palms.
- 5) Disappearance of amphibians followed by return post flooding.

Figure 4.3.1 Canonical Correspondence Analysis (2002/03); ordination plot of *Rana vaillanti* and *Chaunus marinus* with water quality variables. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

Figure 4.3.2 Canonical Correspondence Analysis (2003/04); ordination plot of *Rana vaillanti* and *Chaunus marinus* with water quality variables. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

Figure 4.3.3 Canonical Correspondence Analysis (2004/05); ordination plot of *Rana vaillanti* and *Chaunus marinus* with water quality variables. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

Figure 4.3.4 Canonical Correspondence Analysis (2004/05); ordination plot of *Rana vaillanti* and *Chaunus marinus* with water levels. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

Figure 4.3.5 2003/04 regression of numbers of *Chaunus marinus* with water levels. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

Figure 4.3.6 2004/05 regression of numbers of *Chaunus marinus* with water levels. Ordination axis (x) and series axis (y) are valued in proportion to their corresponding axis vector.

4.3 Behaviour and Ecological Observations

During the flooding period a number of frogs exhibited unusual or unrecorded behaviours and reactions to the flood event. Species that remained undetected during this period included *Craugastor noblei*, *Agalychnis callidryas*, *Dendropsophus phlebodes*, *Hypsiboas rufitelus* and *Leptodactylus pentadactylus*. The vast majority of normal frog breeding behaviour in the forest ceased during the flood and many species disappeared.

Some species were detected more than others. The terrestrial species *Craugastor polyptychus* and *Craugastor fitzingeri* were observed gathering in leaf-axils of *Manicaria saccifera* and *Raphia taedigera* palms. These supposed ‘terrestrial species’, not known to climb, adapted in behaviour and preferred microhabitat to cope with the flood. *C. polyptychus* and *C. fitzingeri* responded to the flooding and climbed high up tree boles and shrubs into the axils of the palms.

Oophaga pumilio was observed to resume typical male-male combat behaviour and it’s vent to vent mating behaviour during flooding. However, this was conducted inside leaf-axils of *Manicaria saccifera*. In the 2003/04 flooding cycle individuals of *O. pumilio* were observed to be removed from their territory by the water flow. Two male specimens were observed to float down the Caño Palma canal on a large floating mat of reeds and debris.

Despite relatively low captures, *Pristimantis diastema* changed little in calling activity and was the only frog that continued in breeding chorus for all inundations in all years.

Bufo coniferus continued breeding activity and gathered in groups at a number of pool locations in the forest. It also continued breeding chorus during 2004/05.

5.0 DISCUSSION

5.1 Experiment 1-An Investigation and Analysis of Environmental Patterns at Caño Palma

5.1.1 Caño Palma Environment Data

5.1.1.1 Historical Climate Data

To assist in describing the annual climate cycle at Caño Palma the Canadian Organisation for Tropical Education and Rainforest Conservation (COTERC), who own and manage the Biological Station, and the Caribbean Conservation Corporation (CCC) Biological Station, based in Tortuguero, were asked to comment on their historical climate records. The results collated came from historical data recorded by local residents and ex-managers of Caño Palma Biological Station (Appendix 3.0).

The historical climate data for Caño Palma Biological Station was patchy across years and often incomplete making comparison between data sets difficult. The information did, however, reveal temperature, humidity and rain levels similar to the data collected in this study. The historical data also graphically showed that inundation of the forest occurred during the rainy season (November-January) and also during heavier rains in May (R. Ballard, P. B. C. Grant & D. Loth *pers. comm.*).

The seasonal climate cycle at Caño Palma was discussed with Sebastian Troeng (previous manager for the CCC Biological Station) and Daryl Loth (previous manager of the Biological Station and resident ecologist of the local area). Troeng and Loth concurred that precipitation and temperature levels were similar in trend to that of the CCC Biological Station, 7km south in Tortuguero, and that differences noted in wind, humidity and temperature between the two Biological Stations were possibly attributable to the CCC's location (i.e. directly next to open ocean).

There was also a consensus of opinion that rainfall was different between the two Biological Stations and that this was influenced by dynamic patterns of offshore

winds. It was concluded that comparison of data between the two Biological Stations would be interesting but outside the scope of this study.

Previous quantitative studies of the local weather are few. Hirth (1963) was one of the first researchers to conclusively measure climate in the Tortuguero area. Hirth recorded average maximum and minimum daytime air temperatures on the beach at Tortuguero as 30.5 and 22.0°C and average maximum and minimum night-time temperatures as 26.2 and 21.0°C respectively. He also measured 3882mm of rainfall at Tortuguero over eleven months. However, other records indicate that figures could be as high as 5000-6000mm per year (Portig 1965; UICN/ORCA 1992).

5.1.1.2 A Description of Climate Using Empirical & Historical Data

The historical results kept by COTERC and the CCC are concurrent with Hirth's (1963) results for the time of year this study was conducted (November to February). When pooled, all three data sets (COTERC, CCC and this study) yielded the following local annual climate cycle description;

- The average daytime temperature at Caño Palma is approximately 26.0°C (23min: 32max) and 70% RH (60min: 95max) and typically stable. Between January and February maximum temperatures vary between 22.0 and 32.0°C, and minimum temperatures, between 18.0 and 24.0°C. January and February exhibit more consistent or stable temperatures with shallow fluctuations between days. Rainfall during January to February is heavy and averages between 500 and 700mm/month. Heavier downpours occur during this time of year and on some occasions exceeded up to 140mm in 24 hours. Generally these heavier downpours are rarer in February reflecting the tailing off of the wetter season.

From February to May maximum temperatures vary between 25.0 to 34.0°C in most years. The historical graphs studied suggested that at this time of year temperatures fluctuated more readily. Data for rainfall during February to April is sporadic but generally varies between 300 and 500mm per month. In May, temperatures increase with maximums between 27.0 and 36.0°C and

minimum records rarely falling below 24.0°C. There is usually a small peak in rainfall in May as the locally known ‘coffee rains’ appear. Rainfall in May is typically between 600-700mm. The coffee rains are seasonal for the whole of the Atlantic coast of Costa Rica and represent a key period for crops to commence summer growth (Kricher 1997).

June, July and August were similar to one another with maximum temperatures between 28.0 and 32.0°C and minimum temperatures around 25.0°C. Rainfall stabilises around 200-350mm with occasional downpours pushing figures as high as 400mm. June is often the driest month of the year. September and October are drier and warmer months with maximum temperatures between 28.0 and 36.0°C respectively and minimum temperatures around 25.0°C. Rainfall was usually at its lowest during these two months, often being between 100-200mm.

November and December are locally the ‘wettest’ months for the Caño Palma area with maximum temperatures rarely more than 25.0-27.0°C and minimum temperatures dropping to 19.0-23.0°C. These months have the greatest rainfall, usually between 700 and 1000mm for each month.

In this study, measurements taken with electronic equipment were tested for differences against traditional mercury bulb equipment to monitor accuracy. Graphically these differences in the 2002/03 season are barely visible but may be attributable to a recording error during hotter weather (4.1). This was recognised as a potential error factor early during recording and it was later learned that sunlight affected the thermocouple used during periods of intense afternoon sunlight. Temperature measurement was then recorded more accurately using electronic equipment after a settling period for the probe next to the wet bulb thermometer. This corrective action improved results.

The only anomaly to the annual climate cycle description was the 2004/05 season flooding cycle. This cycle ended with a further unexpected flood period that occurred due to exceptional heavy rains caused by further saturation of montane areas. The rains were reportedly the worst in 30 years with water tables remaining flooded for

weeks (Anon 2005a). During the heaviest of precipitation the equivalent of one month rain fell in just under 24 hours (350mm) (Figures 4.1.3-4.1.5). Rivers were estimated to flow 25 feet higher than usual. Four people died and thousands were affected. The president declared a state of national emergency (Anon 2005a; 2005b).

5.1.1.3 Historical Hydrological Data

Historical water table measurements did not exist for Caño Palma Biological Station prior to this study. The only previous study made within the area was that of Kelso (1965), who described the tidal cycle that affects the habitats of the Tortuguero estuary. Kelso (1965) measured depths and salinity levels at various points along the estuary and upstream toward the confluence of the three main donor rivers (Rio La Suerte, Rio Agua Fria and Rio Sierpe). He discovered there was little variation in water area from high to low tide because of the unusually steep banks of the estuary (most estuaries have shallow flats at some stage of their tide [Howard 1996]). Kelso (1965) also reported that tidal variation at sea level was approximately 30cm and comprised of two high tides and two low tides in any 24hr period, closely resembling the tide in the southern port of Puerto Limón.

He also found that the tides of the Tortuguero estuary were concurrent with those of the ocean with almost no time-lag, even as far as 5km from the pass of the estuary. Kelso (1965) correlated these observations with rises and falls in salinity, depth and upstream flows from incoming tides. From this information he postulated that as the tides rose the freshwater current was slowed and subsequently backed up as a wedge of dense saltwater was forced upriver along the riverbed. He also found that by high tide this saltwater wedge was at its shallowest below the surface of the deepest parts of the estuary. This layer of dense saltwater halted flow in the top thermocline of freshwater, backing it upstream, but at the same time allowing slight surface level and epilimnion current to continue downstream.

The wide fluctuations in salinity that Kelso encountered during the peak tidal movements indicated internal turbulence at the upper end of the saltwater wedge (Howard 1996). Kelso's hydrological cycle, combined with the low amplitude tides at Tortuguero, high volume of freshwater flow, and maintained surface area of water,

suggest that flow from freshwater donor rivers remains constant during tidal movement and that the saline wedge is a key factor in estuarine tidal rise. However, despite the constant surface area flow of the donor rivers, Kelso recognised that the confluences were also affected by the tidal system because despite continued delivery of freshwater, they would also rise in accordance with the inserted saline wedge.

5.1.1.4 Understanding Caño Palma's Hydrological Cycle

Due to its proximity to the estuary and confluence with the Caño Palacio, the Caño Palma also appeared to be influenced by Kelso's (1965) tidal sequence and exhibited a daily rise and fall in depth that would occasionally change in flow direction from north to south. The organic matter accumulation and released tannins that create Caño Palma's characteristic deep, black, humic-rich canals (Janzen 1974; Myers 1990) changed during flooding and gave way to a stirred mud brown colour variant, as seen in many tropical rivers (Junk *et al.* 2000). This change in colour was an indication that the pass of the Caño Palma into the Rio Suerte is backed up by river water.

This type of upstream influence occurs in Amazonian floodplain forests including; parts of the Amazon River (Mertes 1997; Lima *et al.* 2003), Rio Negro (Ferreira & Stohlgren 1999; Ferreira & Almeida 2005) and river channels near Manaus, Brazil (Junk *et al.* 2000; Whittmann *et al.* 2004), and has been suggested as influential at regional levels in the tropics (Talling & Lemoalle 1998). However, it is a mechanism that remains poorly documented at local levels (Junk *et al.* 2000).

5.1.1.3 An Evaluation of Caño Palma's Climate and Hydrology

At Caño Palma, local level observations from the climate experiment proved useful in interpreting the function of the hydrological cycle, and when combined with Kelso's (1965) more regional Tortuguero information, result in the following inferences;

- Climate fluctuated during the flooding event affecting both the ground water hydrology of the forest and its regular seasonal cycle.
- Severity of the flooding event was governed by increased rainfall combined with spring tidal movements of the Tortuguero estuary.
- The flooding event exhibited cyclical pattern in its occurrence.

It is also indicated by the climate data results that Caño Palma's prominent bi-annual and polymodal flood during its wettest period (November to December) potentially occurs as a result of the following combination of influences when considered with Kelso's (1965) and Myers' (1990) regional descriptions;

- *Lunar cycle* - During November to January the equator is closest to the moon and thus cyclic tidal pull and spring currents are at their strongest. During a new moon this stronger pull ensured that the saline wedge pushed further up the estuary than normal and created a greater volume of water in the estuary. Adjoining rivers are backed up as a result slower flows.
- *Heavy non-localised precipitation* - During November to January periods of heavy rain affected the whole of the coastal tropical wet forest on the Atlantic versant of Costa Rica. This regular heavy precipitation at any altitude higher than sea level may have contributed to the runoff toward the Tortuguero estuarine catchment area during this period.
- *Heavy localised precipitation* - During November to January heavy rains fell naturally as part of the wetter season at Caño Palma and Tortuguero, frequently saturating the local soil structure.
- *Sea breezes and onshore winds* - These wind currents from the ocean bring heavy rain clouds onto the coastal fringe habitats and may have further saturated the water table.

This combination of factors may possibly be the key contributors toward total soil and groundwater saturation of the local coastal habitats of Caño Palma when combined with stronger fluctuating tide tables, persistent heavy precipitation, and percolation from premontane areas.

During the flooding recorded during this study, Caño Palma Biological Station and surrounding areas appeared to act as a catchment area, harvesting water from percolated premontane areas and agricultural run-off further upstream. When the catchment became full, the water table overloaded and the canal flowed high and fast. When the saline wedge was finally inserted via spring tides the canal stopped or reversed in flow direction and finally flooded.

5.1.1.4 A Wider Perspective of Caño Palma's Hydrology

Floodplain boundaries like that of Caño Palma are known to be controlling factors in water cycles of other tropical forests (Brown 1996; Junk 1997; Mertes 1997; Talling & Lemoalle 1998; Junk *et al.* 2000; Lima *et al.* 2003; Ferreira & Almeida 2005). The Amazon and Orinoco are well studied examples (Sioli 1984; Lewis *et al.* 1990; Junk 1997) that exemplify the consequences of seasonal overspill that enlarges water bodies. Egler & Schwassmann (1964) point out that in the Amazon estuary differences in precipitation during wet and dry season have minimal effect on water levels. They believe that flooding is caused by displacement within tidally mixed areas in rivers and estuaries. This may also be the case for Tortuguero estuary. However, from the results of the climate measurements it is clear that this phenomenon is not the sole cause of flooding at Caño Palma.

At Caño Palma heavy seasonal precipitation correlates directly with the onset of flooding and contributed to it by sealing the soil surface layers and/or fully saturating them. The heavy rainfall also increased water level heights of both permanent and ephemeral pools within Caño Palma's forest and the canal periphery. Such a series of multiple flooding influences is not unusual for floodplain boundaries (Mertes 1997). However, for Caño Palma, the action of just a small flood event caused by only one or two, or a misalignment, of flood triggering components, has the potential to raise water tables and create subtle flooding that could influence forest soil and water profiles.

Petts (1995) showed that floods affecting small pocket areas with short pulses, comprising rapid rise and recession, are of little resource value, disturbing floodplain environments. However, on a greater net value across larger ranges these patchily

distributed pockets of flood contribute greatly to the floodplain acting as a conveyance channel rather than storage reservoir (Anderson *et al.* 1996).

Therefore, although Caño Palma's individual flooded area may not be of significant value in size as a floodwater absorbing catchment zone to the whole of the Tortuguero floodplain area, it is possibly joined by other pocket areas that function similarly and together create a matrix of floodplain areas within the whole floodplain unit.

5.1.1.5 A Description of Caño Palma's Hydrological Cycle Using Empirical & Historical Data

The historical data for Caño Palma, used in combination with the data for this experiment, suggest that temperature remains fairly constant throughout the year, a typical feature of lowland wet tropical forest in this region of Costa Rica (Coen 1983; McDade *et al.* 1994; Savage 2002). Rainfall and humidity in lowland tropical wet forests is also typically high on the east coast of Costa Rica due to local atmospheric circulation from ocean to coast that is induced by trade winds (Brenes Vargas & Saborio Trejos 1994). This makes chronological differentiation between wet and drier seasons in this region difficult to classify under Holdridge's (1967) habitat lifezones due to the consistent supply of rain cloud to the coast (Coen 1983; McDade *et al.* 1994). This relegates any descriptions of annual climate seasonality around the Caño Palma area to that of a local description and not specifically 'wet' or 'dry'.

The regular heavy precipitation at any altitude higher than sea level contributes effectively to runoff toward the Tortuguero estuarine catchment area. This type of seasonal discharge reflects the rain cycle of the watershed. As described in Talling & Lemoalle (1998), there are four main types of seasonal variations in rain related discharge;

- True equatorial cycle with two maxima (bimodal).
- Altered equatorial cycle with one maximum (unimodal).

- Humid tropical with one strong maximum.
- Complex cycle of large rivers fed with varying tributaries.

Kelso (1965) showed that precipitation is regular and frequent but also seasonal in volume. Myers (1990) and Ellison (2004a) in their descriptions of the *Manicaria* forest in the area around Caño Palma concur with this finding and describe the local conditions as being wet throughout the year with constant precipitation. However, none of these authors discuss how precipitation seasonally affects high water tables. The most extreme influences of precipitation affecting seasonality in river discharge is in floodplains, oxbow lakes and rain pools of which both unimodal and bimodal discharges can occur (Anderson *et al.* 1996; Talling & Lemoalle 1998; Wetzel 2001).

In their studies, what Kelso, Myers and Ellison did not consider was the potential lunar affects of oceanic circulation and its affects on seasonal environmental change at a local level. This is realised for the tropics (Chutter 1985; Street-Perrott & Perrott 1990), but not fully understood for at many local levels (Talling & Lemoalle 1998). To fully understand this function for the Caño Palma and whether it is correlated with heavy precipitation would take repeated sampling over many years to quantitatively correlate the cycle with flooding and therefore requires more research than is provided in this study. The results in this study, however, are suggestive that the flooding cycle is linked to spring tides through its pronounced reversal of flow upon flooding.

From the above descriptions, observations and discussed mechanisms of the hydrological cycle in this study, and the considerations of climate and hydrological data, it is possible to produce the following description of the hydrological cycle for Caño Palma:

- Caño Palma Biological Station's forest is a *Manicaria* swamp forest with mixed tropical wet forest on higher ground. It exists on the edge of a floodplain boundary and has a seasonal, biannual, polymodal flood cycle.

5.1.2 Water Chemistry Data

5.1.2.1 Water Chemistry Composition of the Caño Palma

The main chemical inputs to tropical freshwaters are linked to riparian edge and physical osmotic movements between them. Inputs are largely affected by surface flow, seepage, weathering of rocks in the drainage basin (omitting human pollutants), organic matter and other break down products from aqueous organisms. Other influences and fluxes generally comprise atmospheric precipitation, exchange of gases across water interfaces and chemical exchange at the water sediment interface (Talling & Lemoalle 1998; Wetzel 2001; Brönmark & Hansson 2005). In reverse, chemical output from tropical freshwaters is generally dominated by surface flow seepage, upper air/water interfaces and lower sediment/water interfaces (Talling & Lemoalle 1998; Wetzel 2001).

The chemical composition of the Caño Palma is undoubtedly influenced by the inputs and output described above, but is also likely to be influenced by its rich organic content. In blackwater canals similar to Caño Palma, persistence of compounds that are resistant to chemical breakdown is common due to the presence of broad classes of humic and fulvic acids (Talling & Lemoalle 1998). These organic acids promote a low ionic content that is only moderate in dissolved organic carbon content, and in turn, different in biological turnover rates, being toxic to some microbes and reducing rates of decomposition (Rai & Hill 1982; Sioli 1984; Talling & Lemoalle 1998). This, in turn, creates a stable chemical composition, that when contaminated, may be slower in its return to a non-polluted state (Talling & Lemoalle 1998; Taylor *et al.* 2002). There are labile compounds such as purines and vitamins also present in blackwater canal systems and these are also likely to have biological importance, possibly by enrichment, but this factor remains poorly understood (Talling & Lemoalle 1998; Taylor *et al.* 2002).

In this discussion of the results of chemical analysis in this study elements that had negligible impact or fluctuation in levels (such as iron) are not discussed in full profile due to their potentially negligible impact on populations of amphibians at Caño Palma.

5.1.2.2 Understanding Chemical Fluctuation in the Caño Palma

Regarding nitrate, the negligible levels present in the water samples taken in this study indicate that the derivation is likely to be from natural sources within water and probably not from sediment stirring or anthropogenic contamination (i.e. agriculture). Subsequently the levels may not be a contamination threat (Burt *et al.* 1993). What little additional nitrate levels occur would likely be utilised by plants and thus further remove any increases during flooding.

Pools within the forest and the floodwaters, comprise mostly rainfall runoff or virtually nitrate free water. Naturally occurring nitrate levels in soil do fluctuate during flooding events in tropical forests but the overall net values of nitrate are often not high enough to cause consequential harm to aquatic life or exemplify eutrophication (Furch *et al.* 1983; Lugo *et al.* 1988; Burt *et al.* 1993; Barrios & Herrera 1994; Kreibich 2002).

Table 5.1.2 Saline content of natural water categories (adapted from information provided in Harrison (1992)).

Water	Salinity %	Salinity mg/l
Fresh Water	< 0.05	< 500
Brackish Water	0.05 - 3.0	500 – 30000
Sea Water	3.0 - 5.0	30000 – 50000
Brine	>5.0	>50000

The limited light available in the blackwater in the Caño Palma may also contribute to its inert nature by slowing plant growth that may otherwise have accelerated in response to a nitrogen increase. This type of solar inhibition has been recorded in blackwaters of the Paraná floodplain in Argentina (Carignan & Planas 1994).

The relationship shown in the Principle Component Analysis (PCA) between salinity (3.2%), carbon dioxide (5.8%) and conductivity (13.4%) is explainable. Where levels of salinity are higher, water tends to be naturally harder, and also higher, in conductivity and carbon dioxide (see Table 5.1.2).

However, conductivity results and salinity did fluctuate minimally during the flooding period and often correlated with rising water levels. Rises in conductivity in other studies have been found to peak initially during the first catchment run-off and were attributed to an increase in dissolved salts (Boulton & Brock 1999). This may explain the slight elevated trend in pH and salinity changes in the regression analysis, although how much this situation applies to Caño Palma is debatable and would require further, more intensively replicated study.

The rise in salinity could arguably be attributed to the change in direction of the Caño Palma's flow (northward) that occurred during flooding. This reverse flow draws in water from the Rio La Suerte that is backed up off of the encroaching saline wedge in the estuary during spring tides. It is therefore possible that some turbulent mixing in the water column could influence the salinity levels further upstream as flows are shunted in and out of the confluence of the Caño Palma and Caño Palacio.

5.1.2.3 The affects of Chemical Fluctuation on Caño Palma's Amphibians

The measurements recorded in this study before, during and after flooding for all sample years barely reached 0.2mS/m conductivity and up to 2.0g/kg salinity (approximately 0.2% seawater). Measurements did not vary significantly between years or during flooding.

Salinity did fluctuate slightly (between 0.6 and 1.8ppt) and this was possibly in response to turbulent water mixing further downstream or on the riparian edge of the Caño Palma. These small fluctuations are well below reported thresholds of 2.0mS/m for developmental problems in amphibians. The effects of increasing salinity have been investigated for a small number of species (Christy & Dickman 2002; Gomez-Mestre & Tejedo 2003; Dunlop *et al.* 2005; Chinathamby *et al.* 2006; Smith *et al.* 2007).

In laboratory and field studies on *Litoria* sp. of frog in Australia, Smith *et al.* (2007) measured conductivity levels and correlated them with salinity. They found no evidence that wetland salinity limited tadpole presence up to about 3000mS/cm

(3.0mS/m) (approximately 6% seawater/freshwater mix). However, they did suggest that human mediated increases in wetland salinity could seriously threaten amphibian populations if salinity levels increased in freshwater wetlands beyond 6000 μ S/cm (equivalent to 6.0mS/m) (approximately 12% seawater/freshwater mix).

Chinathamby *et al.* (2006) reported that *Litoria ewingii* tadpoles suffered significantly reduced survival and poor development in salinities at and beyond about 16% of seawater freshwater mix. Studying a similar species, *Litoria aurea*, Christy & Dickman (2002) found that tadpoles could not develop normally in salinities beyond 4% of seawater / freshwater mix (approximately 2000 μ S/cm or 2.0mS/m) and that survival and developmental rates decreased as conductivity increased beyond about 5.5% seawater / freshwater mix. Mortality in treatments with 10% seawater / freshwater mix or greater was 100%.

Chaunus marinus has been reported to be found in pools with salinity of up to 14000mg/l (20588 μ S/cm) (Liggins & Grigg 1985) and has been observed to biologically increase plasma concentrations to moderate the effects of osmotic pressure (Liggins & Grigg 1985).

Rana esculenta and *Rana temporaria* have been reported to tolerate salinity ranges of up to 7000mg/l (approximately 10294 μ S/cm) (Ackrill *et al.* 1969) and *Rana pipiens* has been reported to die at 35000mg/l (approximately 51470 μ S/cm) (Bentley & Schmidt-Nielsen 1971) and 7000mg/l (Ackrill *et al.* 1969).

Other authors have found similar results (e.g. Viertel 1999) and there appears to be enough species variation in salinity tolerance that more laboratory and field-based studies are required to test tolerances for a broad range of amphibian species. There is a consensus among studies that sudden changes in salinity (like those during a flooding event) may be more detrimental than gradual increases (Nielsen *et al.* 2003). In general, amphibians must maintain hyperosmoticity to their environment and salinities greater than 25% of that of seawater are likely to be problematic for their survival (Mann & Bidwell 1999).

Despite this, some species of amphibian are known to exhibit either an unusually strong, or an acute weakness, in tolerance to salinity (Gomez-Mestre & Tejedo 2003). It is not previously known whether any species at Caño Palma have specific adaptations to increased developmental or physiological resistance to salinity because none have been tested for tolerance prior to this study. It can therefore be suggested that the species studied in this thesis are likely to be tolerant to naturally occurring fluctuations of salinity and conductivity observed during flooding cycles.

With respect to the species that are not studied herein, it is possible that other indirect, more subtle, osmotic stress in the ecosystem may occur from the minor fluctuations in salinity and conductivity. Plants could receive some form of physiological stress as many non-mangal (i.e. not occurring in mangrove habitat) species are known to be stressed under saline conditions (Farnsworth & Ellison 1996). Although investigating this aspect was beyond the scope of this study, a change may exist in the understorey vegetation pattern on island populations of plants at Caño Palma that exist above the maximum flood level. This in turn may alter vegetation composition in the forest and subsequently affect metapopulations of organisms that exist symbiotically with those micro-habitats, including amphibians.

Therefore it can be concluded, based on a comparison with other studies, that there is low level fluctuation in natural levels of salinity and conductivity in the Caño Palma canal during flooding. The upper level thresholds of these chemical components are low enough to not cause serious physiological stress to amphibians.

5.2 Experiment 2-An Analysis of Amphibian Populations from Mark-Recapture Data

5.2.1 Evaluating the Methods Used in Experiment 2

5.2.1.1 Evaluating the Mark-recapture Regime

To successfully interpret the results of this experiment, a test and exhibition of the method appropriateness was necessary. Mark-recapture (M-RC) was used for this study.

The technique is limited by the following assumptions;

- 1) The initial sample is representative of the population and not biased (for example by sex or age).
- 2) Animals captured in the initial sample are marked and the marks are permanent for the duration of study.
- 3) The marked animals are released and become distributed randomly in the population.
- 4) The marking technique does not affect the recapture, survival, or normal behaviour of the species.
- 5) Variation in detectability of different species.

All the above assumption were met for the purposes of this study except 5 (variation in detectability of different species). The first assumption was always met. The frogs caught and marked at any occasion were kept representative of the population because all age classes for each species (adult, sub-adult and juvenile) were recorded. Sex of each species was also recorded for as many of the species as allowed. This was often not possible for sub-adults, juveniles and Hylidae (tree-frog) species (Hylidae are difficult to sex out of breeding condition).

The second assumption was also always met as toe-clipping marking identifies an individual for 2-3 years (Donnelly *et al.* 1994), the duration of the field work component of the study. The third assumption was met as all individuals were released and re-released alive after captures and subsequent recaptures. The fourth assumption was met as there was successful between-year recaptures.

The final assumption 5 was difficult to quantitatively meet as many amphibian species are imperfectly detected during studies in natural environments (Schmidt 2005). Visual encounter surveys in particular are prone to limited detection of all species because of their reliance on surveyor skill and also because some species physical size and habits may be more apparent than others (Vonesh *et al.* 2010). This study attempted to minimise assumption 5 for the species chosen for study by combining both leaf-litter quadrats and visual encounter surveys, and thus

investigating both terrestrial and arboreal niches up to 2.0m in height to maximise detectability of the species in different niches. It is safe to conclude that most of the species surveyed could also have had other survey techniques applied to them such as auditory sampling or pitfall and drift fence trapping (see Heyer *et al.* [1994] and Dodd [2010]) that may have increased results and detection. However, such survey efforts would have equated to unrealistic effort for a solo surveyor and not have been pragmatic under the circumstances of this study (i.e. single surveyor over repeated surveys).

Choice of M-RC technique is governed by the type, cost and requirements of the study and should be considered for appropriateness prior to study (Ferner 2007). A review of the different marking methods for amphibians that were considered for use in this project can be found in Donnelly *et al.* (1994) and Ferner (2007). The methods discussed in Donnelly *et al.* (1994) and Ferner (2007) included pattern mapping, tagging, polymers and pigment marking, banding, branding and toe-clipping. Banding and branding were considered for the study but were thought inappropriate for the range and size of species studied as the method could likely kill juvenile frogs. Tagging and pigment marking was also discarded as a marking method as they can cause movement disruption to juvenile anurans that needed to be successfully marked as part of this study. Pattern mapping was excluded for most *Craugastor* sp. due to their polychromatic and ontogenetic markings (Savage 2002).

Toe-tipping (a variant of toe-clipping) was thus chosen for this study due not only to the other methods unsuitability, but also because it is the least time consuming, most cost effective method and exhibited previous success and reliability among tropical anurans, including the range of species intended for marking in this study (Donnelly *et al.* 1994; Pröhl 2003). Analysing the successful return rate of the toe-tipping methods for this study is beyond its scope. Despite the pros and cons of marking methods, ecologists generally concur that the benefits of knowledge gained for the species concerned in a study, and the considerable risks of marking, far outweigh the negative aspects of such studies (Halliday 1994; Funk *et al.* 2005b; Liner *et al.* 2007).

As presented herein the marking methods used in this study reflect its goals and limits by considering the time scale, training, nature of data, budget, conservation status of target species, public access to the study site and urgency to address amphibian populations (Heyer *et al.* 1994; Funk *et al.* 2005b; Ferner 2007).

5.2.1.2 Selection of Population Modelling Approach

This study analysed three sets of data over 4 months in 3 separate years in order to replicate three times the population levels of amphibians before during and after the flooding event. This replication was necessary to investigate the short and longer term knock-on effect to the population. The remaining eight months of each year allowed natural emigration, immigration, birth and death to occur within all populations of each of the species studied. Arguably because only four months were surveyed intensely over a short period of time, a shorter CJS model may have seemed appropriate.

However, to consider the longer effect of each of the capture histories created, through time, would naturally have had to allow assumptions for natural emigration, immigration, birth and death (Schaub *et al.* 2004). Therefore a classical Jolly-Seber model with robustness from Pollock *et al.* (1990) and Seber (1992) was chosen to over more specialist CJS models.

This model allowed broad assumptions about losses and gains to the population, yet provided a suitable but resistant population estimate with consideration for heavier influences likely to be inferred by immigration and emigration. Its suitability was made possible by the sampling of a significant proportion of the population by a significant series of replicated surveys through time.

5.2.1.3 Addressing Model Assumptions

The following assumptions regarding the use of the Pollock's Robust Open Jolly-Seber model intended for the survey results is discussed below (assumptions bulleted with consideration below).

- Were the marked organisms representative of the population of which inferences are to be made (i.e. marked organisms are a random sample of the population of interest)?
 - The marked organisms were representative as all ages, sexes and size classes for each species studied and included in the analysis.
- Were the numbers of releases known?
 - The number of releases was known absolutely for each species used in the study. The number of non-marked observations was also recorded and can be included in the population count using Pollock *et al.* (1990) robust design to enhance the abundance estimate.
- Was marking accurate with no tag loss, no misread tags and no data entry errors?
 - Marking was accurate, as proven by inter-year recaptures and also due to the use of toe-clipping which could not be lost or misread by the surveyor, thus preventing bias in results (McDonald *et al.* 2003).
- Were all releases made within relatively brief time periods (relative to time intervals between marking periods)?
 - Releases were made immediately following marking of individuals. Sampling occurred on an almost daily basis so recaptures were effectively possible as soon as an individual re-entered the population at a given occasion.
- Were the fate of individual organisms and the fates of organisms in differing cohorts independent (an example of independence would be the banding of a mated pair of adult Canada geese that might behave as one unit, instead of two independent trials)?

- The fates of individual organisms in the study in differing cohorts were considered independent because transects and quadrats that data was collected from did not deliberately centre on a breeding resource or other source of bias and included proven heterogeneous habitat. The habitat was not altered or reduced thus ensuring the population was natural in its composition, and therefore fate, for all cohorts. In the case of the pond samples that included *Rana vaillanti* and *Chaunus marinus*, individuals were assumed to be local to the vicinity of the pond based on their site tenacity both during and between breeding sessions. These species were therefore assumed to be residents of the pond and clearing area. Therefore fates of the individual organisms at all cohorts were assumed to be independent.
- Did organisms in an identifiable class or group have the same survival and reporting probability (parameter homogeneity) for each time interval?
 - Organisms of all classes (ages and sexes) and groups (species) were all reported using the same survey techniques and were treated separately in their analysis. Survival probabilities were not affected by the minimally invasive techniques used. Each survey was conducted at a contiguous time period similar to the last and over the similar flooding cycle period across years.
- Were parameter estimates and sampling covariances based on a good approximation for the model (i.e. the basis for inference is the model, thus, results are conditional on the model used)?
 - The parameters of the study were set and designed around the model to create the best possible chance of good fit.

Despite a claim by Barker (1995) that the Jolly-Seber estimate is limited in its abundance estimator accuracy it has been shown that the estimator suggested by

Jolly (1965) may only be valid if there is limited emigration from the study area but may also remain accurate if emigration is acceptably low or random (Barker 1995).

5.2.1.4 Critique of Survey Method Design

Performing intensive daily survey has been debated by some herpetologists and biologists working to seek population information as potentially applying too much regular pressure by human presence on an amphibian community (Heyer *et al.* 1994; Williams *et al.* 2002). The requirements of the intended sampling protocol (involving mark-recapture techniques, see section 4.3) were such that a high level of repeat sampling was necessary in order to safely generate enough results and give power to predicted estimates of abundance (see Skelly *et al.* 2003).

This study comprised a set of almost daily surveys and therefore a short-term capture series that is appropriate to the abundance models used. A virtually continuous survey is also a better way of increasing the likelihood of sampling all frogs present in the sampling area, whether transient or resident, and gaining better detection (Lebreton *et al.* 1992; Pradel *et al.* 1997; Perret *et al.* 2003; Smith & Green 2005; Amstrup *et al.* 2006). This thus reduces bias in sampling error and in conjunction eases the difficulty of detecting transient amphibians that would otherwise potentially remain undetected in a population (Pradel *et al.* 1997; Perret *et al.* 2003).

Observer differences and experience of surveyor can cause observer bias in detection for VES amphibian surveys (Skelly *et al.* 2003; Solla *et al.* 2005). To avoid this margin of error, surveying was conducted by the author only.

To compromise, and allow the forest to recuperate during each season of survey, fortnightly rest days of 2 or 3 days duration were incorporated into the survey schedule, thus allowing the forest some respite to periods of natural undisturbed activity. The three transects were also alternated in use so that only a maximum of two were surveyed both diurnally and nocturnally on any one day. This enabled intensive sampling of each transect before during and after periods of inundation without constant pressure to each pathway by human presence.

5.2.2 The Abundance and Population Data for Caño Palma Biological Station Pond

5.2.2.1 Abundance Data for *Rana vaillanti* and *Chaunus (Bufo) marinus*

The abundance data (Tables 4.2.1 and 4.2.2) showed that between 2 and 10 *Rana vaillanti* and 1 and 6 *Chaunus marinus* were the most commonly encountered numbers of each species at the Biological Station's pond. The abundance data exhibits a number of trends within these simple counts. For *C. marinus* the number of animals caught over the three sampling year periods was nearly equal for 2002/03 and 2003/04 for the same number of sampling occasions (48).

In 2004/05, although the number of animals caught 'N(i)' increased to 254, this increase was similar in percentage proportion to the extra days sampled. For example 48 N sample occasions equates to 69% of a total N samples occasions of 69 and 162.5 (mean of 2002/03 and 2003/04 years) equates to a 64% of a total N sample occasions of 254. The difference between each sampling occasion of just 4 individuals between 2002/03 and 2003/04 together with a similar proportional percentage increase in animals caught for 2004/05, may indicate a stable population with equal immigration and emigration.

For *Rana vaillanti* the concept of percentage proportions of similar N(i) counts to N sample occasions was not so related and this can clearly be seen with the differences in raw figures of 84, 169 and 243 across sampling year periods respectively. This aspect was likely also affected by sampling effort. Interestingly, the rise in animals caught between 2003/04 and 2004/05 was 63% and also similar to *Chaunus marinus* across year sampling increases between 2003/04 and 2004/05.

For both *Chaunus marinus* and *Rana vaillanti* the marked animals in the population increased by 31% and 17% respectively between 2002/03 and 2003/04. However, marked animals for *R. vaillanti* increased by only 7% between 2003/04 and 2004/05 but by 58% for *C. marinus* in the same year. This may indicate a steady recruitment pattern in *R. vaillanti* but a more erratic pattern in the last sampling year period for *C. marinus*. This possibility is also reflected in the steady increase of newly caught

animals for each sampling year period for *R. vaillanti* and the more fluctuating newly caught animal data for *C. marinus* across sampling year periods.

Observations in the field also support this possibility as more juvenile *Chaunus marinus* were recorded around the pond in 2004/05 indicating death or migration by adult *C. marinus* and replacement by younger individuals. These differences between years in abundance and count data are also reflected in the raw count data tables by increases in mean N for both species.

5.2.2.2 Population Estimates for *Rana vaillanti* and *Chaunus (Bufo) marinus*

Periodic absences in N(i) resulted from days when no specimens occurred, and, for population estimates, where data did not accurately fit the model test, and consequently failed. Absences also resulted in periods when no frogs were found (often during the flooding period) (Figures 4.2.3-4.2.10).

Standard errors in population estimates were not consistent and many fluctuated between and among years. Despite this, some years, for example, *Rana vaillanti* 2003/04 (Figures 4.2.7 and 4.2.8), produced very low error margins in population estimates through time and strong estimates from the computer model. The highest population estimates shown on the graph often exhibit where a series or run of recapture results have successfully been computed through time. This can occur as a population estimate data set is built upon previous capture-recapture information, not just on a current sampling occasion data set (Jolly 1965; Seber 1986; Nichols 1992).

The population estimate data do visually correlate in graphical shape with the N(i) in the visual style of rises and falls in data but do not correlate numerically with a statistical analysis as the estimates are that much higher than the actual abundance count data. The highest population counts at the pond were also recorded during a time when, for both species, conditions were ideal for breeding and calling was recorded to be frequent and regular.

This possibly indicates that both species gather at the pond for breeding when optimum numbers of frogs and toads are chorusing. It also is suggestive at a

numerical presence level, that both species are halted in their breeding activity and that both species groups exhibit a time lag in returning to the pond and recovering to normal behaviour. This disturbance and recovery pattern, at the height of both species (*Chaunus marinus* and *Rana vaillanti*) breeding period, has not previously been documented for either species in riparian floodplain environments.

The unstacked analysis of variance (ANOVA) test in MINITAB exhibited large variance in Pollock Open Jolly-Seber population estimates between years and demonstrated influential variance in results (e.g. $P = 0.085$ for *Oophaga pumilio* in 2004/05 [Figure 4.2.13]). Whilst this ANOVA test was technically flawed by insufficient population estimate output and non-normally distributed data, it demonstrated that further statistical analyses of the differences was not necessary.

5.2.3 The Abundance and Population Data for Caño Palma Forest

5.2.3.1 Pollock Open Jolly-Seber Population Estimates for Forest Species

Oophaga pumilio was the strongest of all recaptured species data sets because it had the most model fits for the Pollock Open Jolly-Seber population estimates as well as having most recaptures and inter-year recaptures (Figures 4.2.13 and 4.2.14; Tables 4.2.7 and 4.2.8). The remaining forest species that also exhibited recaptures in their data all failed in their suitability to be compared in their variability (Tables 4.2.6 and 4.2.7). *O. pumilio* results that did not provide adequate successful population test output to examine variability between years may have required a larger sampling protocol to gain greater species detection.

However, it is more likely, that populations of *Oophaga pumilio* were over and above the territories or resource carrying capacity for the species. This may indicate that a number of *Oophaga pumilio* marked during the study were either nearby residents exhibiting ranging behaviour or vagrants that migrated from wider territories in the *Manicaria* forest temporarily to the sampling area.

The remaining forest species that also exhibited recaptures in their data all failed in their suitability to be compared in their variability (Tables 4.2.6 and 4.2.7). It is

difficult to comment on why many of the forest species failed to produce satisfactory population estimates using the Pollock Open Jolly-Seber method without rigorously testing the model through hypothetical data sets in comparison with those herein.

However, some forest species did fail to produce adequate recaptures (e.g. *Scinax elaeochrous*). Some were also simply too low in abundance to provide adequate output (e.g. *Craugastor noblei*). These particular species could have been cryptic, remained undetected, or were simply not highly abundant in the area sampled to gain full results capable of fulfilling the Pollock Open Jolly-Seber model. This possibility was demonstrated on data for *Leptodactylus melanonotus*. *L. melanonotus* exhibited equal capture (N_i) and equal newly captured (U_i) results. When combined with no recapture results or too few results the model failed to give a good fit to produce a range of population estimates (Figure 4.2.15).

5.2.3.2 Petersen-Schnabel Population Estimates for Forest Dwelling Species

Despite the failure of the Pollock Open Jolly-Seber model to give satisfactory understanding of populations of all species through time, other inferences were able to be made about the population abundance estimates and abundance count data. To compensate for this reduction of good model fitting by the data the traditional Petersen-Schnabel population test was conducted to examine total annual population abundance of each forest species, for each yearly sampling period year. The Peterson-Schnabel estimator of abundance is a population estimate of the total population based on an assumption of a closed population in a snap shot of time. It calculates the whole population whereas the Pollock Open Jolly-Seber is an actual population estimate for a point period in time in a localised area based on direct recapture and previous recaptures through time.

The results of the Peterson-Schnabel estimates in Table 4.2.9 exhibited contrasting results with the Open Jolly-Seber population estimates. This was primarily due to the differences in the two estimating techniques. When the Petersen-Schnabel estimates were compared with complete abundance (N_i) forest data a more realistic comparison was observed (Table 4.2.10). This comparison suggested that as N_i results for species rose then the Petersen-Schnabel estimate also rose. This

observation held true for most species, in most years, with *Craugastor fitzingeri* and *Craugastor polyptychus* exhibiting abnormal differences that did not portraiture a simple graphical trend.

5.2.4 An Evaluation of Caño Palma's Amphibian Populations

5.2.4.1 Ecological Observations from the Abundance Data

Chaunus marinus and *Rana vaillanti* abundance data varied during the flood. Returns by marked individuals for *C. marinus* (133 in total) were higher than that of *R. vaillanti* (90 in total) and this was reflected in the total abundance of *C. marinus* being higher than *R. vaillanti*. Using the individual capture day estimates, the flooding event was able to be seen as a gap within the population data where estimates were zero.

Data between years did not exhibit a trend of decline for *Chaunus marinus* or *Rana vaillanti* over all three sample year periods and therefore it was not possible to comment on a population trend that may lead to a decline in the local metapopulation. The abundance data suggests that a decline is to the contrary and that populations remained stable in what can only be described as normal circumstances before and after the flooding event (Table 4.2.10). However, the individual capture histories and abundance data also show where captures ceased and frogs disappeared due to flooding. This is exhibited clearly from the data shown for both *Chaunus marinus* and *Rana vaillanti* (Figures 4.2.1-4.2.8).

The N(i) abundance data counts and observations of the forest species in this study differ from those in previous studies investigating abundance of amphibians in tropical forest and pond environments through time, although proportionally the results are similar for each species. *Craugastor fitzingeri*, *Craugastor polyptychus* and *Oophaga pumilio* (in order of highest abundance respectively) are by far the most frequently observed species in Caño Palma's forest. This observation agrees with previous studies of these species of leaf-litter amphibians (Scott 1976; Allmon 1991; Watling & Donnelly 2002). This was also noted in the proportionally ranked abundance data that compared a number of species with data from Scott (1976). The

rank abundance data was only possible for 7 species at Caño Palma; *Bufo coniferus*, *Oophaga pumilio*, *Craugastor noblei*, *Craugastor persimilis*, *Craugastor polyptychus*, *Pristimantis diastema* and *Rana vaillanti*. The seven species were not similar in actual abundance totals per study (Figures 4.2.11a/4.2.11b) and were also different in proportional ranked abundance (Figure 4.2.17). However, the least abundant frog species (*Craugastor noblei* and *Rana warschewitschii*/*Rana vaillanti*) did show similar rank abundance levels, indicating that these species occupy similar dominant population abundances at La Selva and Caño Palma Biological Station's forest habitats. The slope of proportional abundance was also quite similar in shape for both La Selva and Caño Palma Biological Station's results, suggesting that at least proportionally, species dominance is similar. More surveyor effort and a larger, more extensive data set may clarify this.

Comparing simple N(i) count data between sampling years showed that flooding does alter the balance of amphibian abundance temporarily and that abundance remains relatively low during the wet season. Season, has been shown to influence richness and relative abundance of amphibians (Lieberman 1986; Aichinger 1987; Watling & Donnelly 2002). In this study, Caño Palma's amphibian abundance was clearly affected by the seasonal flooding cycle. When floods rose, the abundance of amphibians plummeted and slowly returned when floodwater receded.

In the late dry season of lowland Atlantic forest in Costa Rica (August for Caño Palma) a distinct flush of juvenile *Craugastor polyptychus* was seen on the forest floor. This increase in juvenile abundance may be indicative of strategic breeding by *C. polyptychus* (Donnelly 1999). During the dry season modest increases in leaf-litter encourage population explosions of leaf-litter prey items for the frogs. This factor may encourage higher intensities of breeding (Donnelly 1999).

Increased abundance of terrestrial species of tropical amphibians during the dry season has been shown to correlate with increased leaf-fall that promotes increased arthropod abundance (Toft 1980; 1981; Lieberman 1986; Allmon 1991; Fauth *et al.* 1989; Watling & Donnelly 2002; Watanabe *et al.* 2005; Van Sluys *et al.* 2007).

The flooding possibly amplifies the pressure on naturally lower population abundance levels during the wet season and may reduce populations of arthropods by interfering with arthropod lifecycles. This aspect may have an affect on anuran populations at Caño Palma in the short-term, during and after the flood cycle and would invite interesting further study.

Other observers have recorded peaks in amphibian abundance during the wet season (Scott 1976; Allmon 1991; Vonesh 2001) and in particular during heavy rainfall (e.g. Duellman 1995). This is a phenomenon that is most probably related to the phenology of reproductive activity as well as environmental tolerances of individual species (Donnelly 1989b; Donnelly & Guyer 1994; Stewart 1995; Watling & Donnelly 2002).

For Caño Palma, this situation is arguably reflected in the healthy populations of *Chaunus marinus* and *Rana vaillanti*. Both these species are known to commence breeding behaviour upon heavy rainfall in response to reproductive resources like ponds becoming more suitable for breeding use (Ramirez *et al.* 1998; Lever 2001). Whether the pond is their only breeding resource is debatable. There are some temporary pools in edge habitat around the Biological Station in the wet season that could support both *C. marinus* and *R. vaillanti* spawning.

Richter & Seigel's (2002) work on *Rana sevosa* in the coastal plain forests in southern Mississippi discovered that not all *R. sevosa* reproduced every season and also showed that many had failed reproductive years or skipped breeding seasons. This relaxed reproductive effort also occurs in Caño Palma's population of *Rana vaillanti*. As demonstrated in the data herein (Figures 4.2.1-4.2.8), not all marked *R. vaillanti* returned every year to the Biological Station pond, or at least they were not detected, despite detection being as complete as possible from intensive survey and surveyor effort.

Intermittent breeding years are known for a number of amphibian species globally and this may be linked to the level of foraging success that may be required to achieve required body composition for breeding or sexual maturation (Wells 2007). Whether the intermittent breeding behaviour shown by *Rana vaillanti* is typical of

the species or linked to body mass/maturation remains to be studied. Many Ranid frogs also use multiple ponds through and between years and this may also be a reason for the absence of some individuals during certain years (Berven 1990; Tarkhnishvili & Gokhelaashvili 1999; Bosch & Martínez-Solano 2003; Watson *et al.* 2003; Funk *et al.* 2005a).

Additionally, the number of returning *Rana vaillanti* found at the pond may be affected by survivorship. Ramirez *et al.* (1998) observed populations of *R. vaillanti* in Mexico and estimated survival duration of eight months for adult frogs. In this study, survival was longer for specimens that returned to the pond for two or more seasons, with some marked frogs proving that longevity was 12 months and possibly more. Other return rates for Ranids can be as low as 16-22% (Richter & Seigel 2002) or as high as 98% (Pope & Matthews 2001; Vasconcelos & Calhoun 2004). The movement patterns exhibited by individual *Rana vaillanti* are relatively unknown and did not form part of this study. However, in other studies of pond breeding, Ranid movement exhibited a randomised pattern of dispersal from ponds that was driven mostly by habitat dynamics, density dependence and prey resource, with clear differences exhibited between sexes (Dodd & Cade 1998; Pope & Matthews 2001; Vasconcelos & Calhoun 2004).

The population of *Chaunus marinus* at Caño Palma Biological Station pond exhibited patterns of fluctuations and stability similar to *Rana vaillanti* (Figures 4.2.1-4.2.8 and Tables 4.2.1-4.2.4). The highest counts of animals caught were in the 2004/05 season (254 - *C. marinus*; 243 – *R. vaillanti*). *C. marinus* was also equally tenacious to the breeding pool, living close to the Biological Station pond and breeding opportunistically. Recruitment of new individual toads to the existing population was, however, lower for *C. marinus* (Mean 25.6 across all years; Table 4.2.1) than *R. vaillanti* (Mean 27.6 across all years; Table 4.2.2) and it is possible that turnover of individuals was lower across years for *C. marinus*.

In studies of *Chaunus marinus* in Australia, the species exhibited reduced site fidelity, with annual and inter-annual recaptures that were lower than in this study (Margarita & De Leo 1998; Schwarzkopf & Alford 2002). This results in increased turnover and expansion within a population. It is possible *C. marinus* exists in its

natural environment it exhibits sustainable populations that occur in sympatry with other pond breeding species (Zug & Zug 1979), as exhibited here with *R. vaillanti*. In introduced environments its tenacity toward a breeding resource is possibly reduced and its behaviour becomes more nomadic, thus increasing migration (Lever 2001; Schwarzkopf & Alford 2002).

C. marinus usually frequents areas that have high abundance of prey items (Zug & Zug 1979). Areas with high prey abundance are also usually correlated with breeding resources in disturbed and edge areas, which may account for the species' lack of presence in Caño Palma's forest, although this is somewhat speculative. What is uncertain is why juvenile *Chaunus marinus* did not occur in certain plots within Caño Palma's forest. This could be because conspecific juveniles are at risk from general predation and also from cannibalism by adult *C. marinus* (Zug & Zug 1979).

Many tropical amphibians spend a high proportion of their lifetime at less than adult size and large proportions of individuals (up to 80%) within populations may be sub-adult (Crump 1974; Donnelly 1989b; Moreira & Lima 1991; Donnelly 1999; Watling & Donnelly 2002). Juvenile amphibians often disperse to greater distances from wetland edges than adults because competition with adults may be greatest near wetland features (e.g. pools) (Loman 1981; Duellman & Trueb 1986; Trenham & Shaffer 2005; Wells 2007). It is possible at Caño Palma that juvenile *Chaunus marinus* do not expend energy on annual breeding migrations to the breeding resource and/or that juveniles disperse to other local populations.

5.2.4.2 Summary and Critique of the Population Data

At Caño Palma local populations of amphibians may have fluctuated in response to changes in local habitat and local climate conditions. This was exhibited with some evidence of disrupted population abundance at the time of flooding. Many amphibians disappeared, reduced their activity during flooding, and thus were not found during surveying. This type of interference within population abundance data and results is referred to as local 'noise'. Local noise increases local extinction rates but at the same time reduces extinctions at larger landscape scales by the enhancement of diversity in evolutionary survival adaptation (Halley *et al.* 1996;

Hanski & Gilpin 1997; Heino *et al.* 1997; Heino 1998; Carlson & Edenhamn 2000; Lopez & Pfister 2001; Bosch *et al.* 2004; O’Grady *et al.* 2004). Amphibians are often not evenly distributed or stable in abundance in terrestrial habitats surrounding wetlands (Rodríguez 1992; Hartel *et al.* 2006; Rittenhouse & Semlitsch 2007). The flooding cycle at Caño Palma may have contributed to such uneven distribution and abundance or created loosely connected micro-populations. Temporary ‘local noise’ and uneven distribution at Caño Palma Biological Station pond and forest may possibly place pressure on species that are less tolerant of such harsh climatic events. This may be a factor that influenced population structure of several species at Caño Palma and may also be why such species are more populous in other lowland tropical forests (e.g. *Craugastor persimilis*) (McDade *et al.* 1994).

5.2.5 Ecology and Behaviour of Caño Palma’s Amphibians

5.2.5.1 Behaviour Response by Amphibians to Flooding

The fluvial processes that allow inundation to occur at Caño Palma are important for sustaining the composition of amphibian species along river corridors and floodplain forests. Over short time-scales (<100 years) it is likely that changeable flooding cycles, like that at Caño Palma, promote exchange of materials and organisms among the mosaic of habitats present and thus assists in regulating biological diversity and function (Bayley 1995).

This exchange was evident among a range of taxa during this study at Caño Palma Biological Station, but especially evident for Amphibia. For Caño Palma the flood pulse is often of short enough duration (percolating to normal levels in 2 weeks) to allow many species to ‘weather the storm’ as opposed to directly or physiologically adapting to it. Such disturbance regimes, and the river’s response to them, are natural components of healthy riverine ecosystems (Janzen 1974; Brunke & Gonser 1997; Naiman & Décamps 1997). At Caño Palma Biological Station pond, *Chaunus marinus* and *Rana vaillanti* coped with the flooding event by evasive action whilst still maintaining territories. Often, *C. marinus* would continue to call into the flood period and still engage in spatial territory defence on the last islands of land before complete flooding of the pond (see Plate 5.2.5.1a and 5.2.5.1b).

Plate 5.2.5.1a Caño Palma Biological Station grounds pond before flooding.

Plate 5.2.5.1b Caño Palma Biological Station grounds pond during flooding.

When the pond became fully saturated, *Chaunus marinus* would cease breeding activity, disperse to the edge of the Biological Station grounds and remain undetectable. It is possible that they remained dispersed inside thick forest edge vegetation until the flood levels dropped. However, *C. marinus* is known for exhibiting site fidelity to breeding resources (Brattstrom 1962; Zug & Zug 1979; Strüssmann *et al.* 1984; Carpenter & Gillingham 1987; Lever 2001). The species is also known to travel long distances (up to 862m [Zug & Zug 1979]) in getting to breeding and foraging grounds. Carpenter & Gillingham (1987) studied water hole fidelity by *C. marinus* and also found that the species hydroregulates itself in response to drier environmental conditions (i.e. it actively seeks water in response to drought). Such behavioural adaption by *C. marinus*, considered with the observations in this study, concur with other authors and suggest that flexibility in its behaviour patterns in response to changing environmental gradients is key to its colonisation success (Lever 2001).

Rana vaillanti behaved in a similar manner although it was often the first of the two species to leave the pond and disperse. Interestingly, it was only when flood waters had dropped completely for several days that both species returned to the pond to resume normal territorial and breeding activity. Breeding resource fidelity is known for *R. vaillanti* (Savage 2002) but not under the circumstances of regular annual spatial displacement by flooding. This study therefore confirms that this species is also dynamic and tenacious in its breeding resource choice.

A number of transient species were recorded visiting the Biological Station pond and grounds during the survey periods, but these species only occurred sporadically, did not remain resident, and therefore were not included in the final Jolly-Seber analysis as the model would not fit for only single encounters. Transient species included *Bufo coniferus*, *Dendropsophus ebraccatus*, *Dendropsophus phlebodes*, *Hypsiboas rufitelus*, *Scinax elaeochrous* and *Smilisca baudinii*. *Oophaga pumilio* was also an occasional visitor to ornamental bromeliads in the Biological Station grounds but was regarded as a transient for the purposes of this study as the bromeliad resource was not a naturally occurring feature but was placed in the gardens by staff to encourage *O. pumilio*.

Bufo coniferus visited the Biological Station pond in the 2003/04 studies. During its brief exploitation of the pond, males attempted to outcompete resident *Chaunus marinus* and *Rana vaillanti* during the onset of the 2003/04 rains. *B. coniferus* was unsuccessful for the most part in vocal territory dominance but managed a brief breeding period with several adults in the pond producing a small amount of viable spawn that successfully hatched.

Development of tadpoles of *Bufo coniferus* was successful and metamorphs emigrated from the pond. Interestingly, although individual recognition was difficult some of the metamorphic young toads that had been toe-tipped occurred in the capture zones in the Biological Station grounds on subsequent nights. Three of these clipped toads were briefly relocated on transect B approximately 200m into the forest. This confirmed that *B. coniferus* juveniles dispersed outside of the breeding arena, possibly to complete development and maturation to adulthood in a different and possibly larger territory.

This type of emigration is similar to that of other pond breeding species in temperate climates (Pough *et al.* 1998; Beebee & Griffiths 2000; Rothermel 2004; Funk *et al.* 2005b). In this study *Bufo coniferus* was not seen in 2004/05 and was therefore regarded as a transient species to the pond. It is possible, however, that *B. coniferus* would re-colonise the Biological Station pond again. Whether the newly metamorphosed toads that emigrated from the pond returned is undetermined. Amphibians are thought to have low juvenile dispersal rate (Blaustein *et al.* 1994b), although this may not apply to all species (Alford & Richards 1999; Marsh & Trenham 2001). *B. coniferus* juvenile dispersal is unknown.

For pond breeding species at the Biological Station grounds, social and environmental factors may have acted simultaneously to influence choice of reproductive, foraging and habitat resources (Pough *et al.* 1998; Wells 2007). For most amphibians, whether a site is accepted for breeding ultimately depends not only on the assessment of mortality risks to offspring but also on the sex and spatiotemporal context of the decision maker (Wells 2007). This was shown in a study by Murphy (2003) where adults of *Edalorhina perezii* selected the safest pools

for offspring based on two biotic risks of different magnitude: insect predators and conspecific competitors.

For *Chaunus marinus*, *Rana vaillanti* and *Bufo coniferus* the flooding did not appear to disrupt these factors or disrupt the species' eventual return to normal breeding activity. It is therefore possible to conclude that all three species of pond breeding amphibians at Caño Palma Biological Station grounds in this study exhibited high site fidelity to the pond as a breeding resource.

In Caño Palma's forest similar behavioural responses to the flood were observed as those recorded for *Chaunus marinus* and *Rana vaillanti*. However, not all forest dwelling species were encountered during the flood. Some species remained elusive throughout the flooding cycle. Species that remained undetected included *Craugastor noblei*, *Agalychnis callidryas*, *Dendropsophus phlebodes*, *Hypsiboas rufitellus* and *Leptodactylus pentadactylus*. Presumably these species remained hidden or migrated to drier islands of land in the forest outside or beyond the study area.

Species appeared to be affected in different ways, depending on ecology, life history and behavioural adaptation. Most arboreal species or those known to climb to higher perches from terrestrial refuges were observed to move into the trees, lianas and vines. No Hylid species and *Pristimantis diastema* were observed on transects survey or tree axil searching during flooding, possibly due to them climbing higher into the canopy.

Some less fortunate terrestrial species without climbing adaptation, ability or experience would cling to the base of vegetation at the waterline. This would likely place them at risk of predation from larger fish, predatory birds and crocodilians. Some of these supposed 'terrestrial species', not known to climb, adapted in behaviour and preferred microhabitat to cope with the flood. Notable examples were *Craugastor polyptychus* and *Craugastor fitzingeri*. These two species responded to flooding by climbing high up tree boles and nestling into the axils of *Raphia* and *Manicaria* palms.

Craugastor fitzingeri is adept at climbing and is often found at perch heights of up to 1.6m in the forest on tree buttresses and vegetation during nocturnal activity (Miyamoto 1982; Höbel 1999). In normal territorial behaviour *C. fitzingeri* males hold higher elevated perches, with females and then juveniles in descending height (Höbel 1999). During nocturnal surveys of flooded forest, *C. fitzingeri* were not located in their typical hierarchal structure and all age classes were found on vegetation at varying heights. During diurnal surveys in flooded forest specimens were scarcely found and it is possible the frogs may have climbed higher than usually seen. Some specimens were also found concealed within *Raphia* and *Manicaria* axils and actively foraging within them. These observations are new behaviour, different from previous studies and different from normal behaviour observed for the species at Caño Palma (Miyamoto 1982; Höbel 1999).

Unusually *Craugastor polyptychus* was also observed to climb tree boles and congregated in small groups of up to four individuals in *Manicaria* and *Raphia* axils. Individual frogs were encountered buried within leaf-litter and debris caught in palm frond axils by the palms elongate trichomes that protect new fronds. Some individuals were observed foraging and others were in a dormant state. *C. polyptychus* is not known to regularly climb and its behaviour during flooding may possibly be an avoidance response to predators. The concept of terrestrial species of frog exhibiting tendencies to climb is not new phenomenon. Some examples where species of terrestrial amphibians that are adapted to arboreal lifestyles or have been observed climbing include:

- *Bufo terrestris* in Georgia, U.S.A. was observed using an arboreal tree cavity for a refuge (Kornilev 2007).
- *Bufo bufo* in Cornwall, U.K. was observed foraging at some height on Lamiaceae shrubs (Pincheira-Donoso 2007).
- *Bufo valliceps* in Texas, U.S.A. was observed at heights of 2-5m in Oak Tree (*Quercus virginiana*) bole holes (Neill & Grubb 1971).
- *Aneides ferreus*, *Aneides lugubris*, *Pseudacris regilla* and *Dicamptodon ensatus* have known arboreal habits and were all observed occupying nests of *Arborimus* sp. voles at height in Oregon, U.S.A. (Forsman & Swingle 2007).

- *Aneides vagrans* is a highly arboreal species and was found residing up to 90m in canopy of old growth Redwood forest in California, U.S.A. (Spickler *et al.* 2006).
- *Aneides aeneus* was observed to seasonally use hardwood trees and rocky outcrops in South Carolina, U.S.A. (Waldron & Humphries 2005).
- *Eleutherodactylus melanostictus*, *Eleutherodactylus crassidigitus*, *Eleutherodactylus noblei*, *Eleutherodactylus biporcatus*, *Eleutherodactylus diastema* and *Eleutherodactylus fitzingeri* (old synonyms) were all found to exhibit varying degrees of nocturnal arboreal climbing between 10cm and 183cm, related to calling perches by male specimens in Costa Rica (Miyamoto 1982).
- A number of Hylid frogs of the genus' *Hyla*, *Osteocephalus* and *Phyllomedusa* were observed to descend completely from arboreal habitat following FriaJe (rapid cold changes in wind currents) weather changes in Madre de Dios, Peru (Doan 2004).
- Arboreal movement and related parental care lifecycle has been documented for *Oophaga pumilio* in Costa Rica (Young 1979).
- Arboreal habitat use and gliding as rapid response from predators and for general descent movement has been documented for some species of Hylid frog and a few select species of terrestrial frogs in Costa Rica and Panama (Stewart 1985; Roberts 1994; Duellman 2001).
- *Alytes obstetricans*, *Bufo bufo* and *Rana temporaria* were all observed on multiple occasions climbing trees to rehydrate among epiphytic moss during the dry season of oak forest in Lizaso, North Spain (Gosá 2003).

The behavioural activity surrounding use of arboreal habitats by amphibians climbing has been considered for various species and has been suggested as being attributed to a restriction in preferred habitat available (Neill & Grubb 1971), an advancement of foraging niche area (Pincheira-Donoso 2007), specialist microclimate adaptation (Spickler *et al.* 2006), adaptation of shelter requirements (Pincheira-Donoso 2007; Forsman & Swingle 2007; Kornilev 2007), adaptation of hibernation refuges (Waldron & Humphries 2005), adaption to changes in climate (Doan 2004) and choice in perch height calling posts (Miyamoto 1982).

The observations made in this study suggest that many species of amphibian at Caño Palma respond to flooding for survival. This was demonstrated particularly by terrestrial species when they were observed to float between drier islands of land between flooded areas or congregate on such islands in clusters. Some of these terrestrial species, notably *Craugastor polyptychus* and *Craugastor fitzingeri* also utilised this time in proximity to one another as an opportunity to reproduce and to feed, suggesting that opportunistic survival instincts may contribute to the success of terrestrial species on an annual basis. The flooding may assist in fitness selection traits during clustering on islands, and the increased availability of food, may have provided much needed energy for active reproduction. Fitness selection during flooding would make interesting further study for *C. polyptychus* and *C. fitzingeri*.

That the response of climbing behaviour witnessed in this study is prompted by flooding is likely. Several of the species studied in this project (notably *Craugastor polyptychus*, *Craugastor noblei*, *Oophaga pumilio* and *Pristimantis diastema*) tend to inhabit and forage around tree buttress microhabitats and use the increased leaf-litter accumulation around tree bases for shelter, territory and breeding (Wells 1981; Gibbons 2003; Whitfield & Pierce 2005). These species also show substantial fidelity to these microhabitats (Miyamoto 1982; Höbel 1999; Whitfield & Pierce 2005; Han *et al.* 2007). Tree buttress microhabitats are also slightly higher in elevation than leaf-litter on the forest floor, due in part to the tree buttresses, and therefore are likely to form the final islands of available terrestrial refuge during a rising water table.

An observation of breeding behaviour by *Oophaga pumilio* occurred during flooding in sample year periods 2002/03 and 2004/05 when some individuals congregated in *Manicaria saccifera* and *Raphia taedigera* axils. *O. pumilio* was observed to continue its typical male-male combat regime and its vent to vent mating behaviour during flooding. Amphibians are known to forego breeding during years in which the climate and habitat conditions are unfavourable (Pechmann *et al.* 1991; Heyer *et al.* 1994). It seems likely that the flood conditions brought *O. pumilio* individuals in closer contact enabling the observed mating behaviour.

Craugastor noblei is known to ascend foliage and trees (Miyamoto 1982) but both *Craugastor persimilis* and *Craugastor noblei* were not found during flooding which may be due to their generally low abundance in the forest during normal water levels. Neither species was found in leaf axils and it is not known whether either species ascended into the canopy, migrated or hung onto lower vegetation during the flood.

Despite its relatively low captures, *Pristimantis diastema* changed little in calling activity and was the only frog that exhibited a continuation in breeding chorus for all inundations in all years. It was apparently unaffected by the flood but did not call more, or less frequently, in accordance with reduced noise interference from other nocturnal callers that would otherwise be breeding in normal non-flooded conditions. Male *P. diastema* are tenacious to their nests and some calling sites (Ovaska & Rand 2001) and as such this may assist in their relocation to specific resources after the floodwater recedes. This species is also known to occur in the leaf-litter layer during the day and ascend to breeding posts by night (Savage 2002). It possibly spent the daytime hidden among vegetation above the waterline.

Other forest species that suffered during the flood included less arboreal terrestrial species such as *Leptodactylus pentadactylus* and *Leptodactylus melanonotus*. Both these species were observed to commence breeding activity upon the onset of heavy rains. In all years there was a strong arrival of *L. pentadactylus* in the Biological Stations grounds and in edge zones in Caño Palma's forest that was likely in response to ideal breeding and dietary conditions. However, calling, presence and breeding activity all ceased when the flood arrived. Both species were observed floating in flood water and literally presented themselves at risk from aquatic predation. Some individual *L. melanonotus* were observed to dive under water in response to disturbance. Others simply floated in liquid space apparently undeterred by predation risk and were easily captured for M-RC. Whether the cooler temperatures of the flood water reduced metabolism and activity in the individuals remains unanswered.

Bufo coniferus was another species that commenced breeding activity upon the onset of heavy rains in Caño Palma's forest. However, it differed in its reaction to the forest flood. Instead of ceasing breeding activity *B. coniferus* continued to gather in

number at pool locations in the forest. As these pools became more connected with the rising flood males gathered and called to attract groups of up to 20 or more toads. Some toads were successful in breeding but the survival of tadpoles was very much determined on the hydroperiod length of the pool. When the flood receded many tadpoles died from desiccation in ephemeral pools.

Synoptic niche sharing is relatively common among pond breeding amphibian as many species share similar breeding resources (Duellman & Trueb 1986; Stebbins & Cohen 1995; Pough *et al.* 1998; Wells 2007). Species of tropical amphibian do coexist (Crump 1974; Donnelly & Guyer 1994) but may not always share the same microhabitat or dietary elements (Van Sluys & Rocha 1998; Menin *et al.* 2005). The observation of species of terrestrial adult anurans congregating in palm tree axils represents an example of aggregation behaviour that has benefits and risks. The benefits may include;

- Increased likelihood of meeting a conspecific sexual partner (e.g. for *O. pumilio*).
- Increased prey resource in a confined area (i.e. increased invertebrate abundance sharing the same temporary resource).
- Mutual physiological thermoregulation (i.e. when temperatures drop through sustained rainfall).

The risks of such an aggregation may include;

- Increase susceptibility for predation.
- Interspecific competition for resources.

In this study, mass congregations of *Oophaga pumilio*, *Craugastor fitzingeri*, *Craugastor polyptychus* and *Pristimantis diastema* were observed in *Manicaria* and *Raphia* palm frond axils. This type of behaviour has not previously been documented for these three species. Whether the species that engage in arboreal behaviour during the flood are triggered into mass congregations by olfactory cues is debatable. *Oophaga pumilio* is known to have preference for odours that emanate from its own

residential territory (Forester & Wisnieski 1991). Investigation into the distributional movement of *O. pumilio*, other flood affected species and their processes of orientation choice would make interesting further study.

During one flood event a different kind of influence from the flooding was seen for two individual *Oophaga pumilio*. During all sample period years (2002/03, 2003/04 and 2004/05), floating and partially submerged seed masses would be drawn into or exchanged with the saturated leaf-litter and forest debris when flood waters rose. Forested areas and root buttress systems would trap some of these debris mats and when the flood receded they would float through the forest and out into the arterial canal.

In the 2003/04 flooding cycle individuals of *Oophaga pumilio* were watched to be removed from their territory by the water flow. Two male specimens were observed to float down the Caño Palma on a large floating mat of reeds and debris. Interestingly one male still called but only for a brief period of less than one minute. Whether the two *O. pumilio* were in territorial dispute or simply had been located on the debris when flooding displaced them from terrestrial refuge remains undetermined.

Floating mats of vegetation are a common feature in other inundated *varzea* habitats in Amazonia (Junk 1997). These mats are known for influencing the distribution and function for riparian plants and invertebrates by carrying seeds and/or larvae off to new areas (Sioli 1984; Junk 1997; Ellison 2004a; Yanoviak *et al.* 2006). Their affect on amphibians is not documented though and observations made herein may be the first of their kind.

Interestingly the only specimen of the rarely encountered, high canopy Hylid frog *Cruziohyla calcarifer* known from the Biological Station was found during the 2004/05 flood inside a reed bed floating in the Biological Station grounds. This species is rarely seen and is always encountered in high canopy. Whether the frog had jumped into the canal for migration or had been forced from refuge is not known.

Another high canopy Hylid species of tree-frog was also observed exhibiting migratory behaviour during flooding. In sampling period 2002/03, a *Smilisca baudinii* (toe-clipped marked LF3) that was marked in Caño Palma's forest was observed on a pathway on the opposite side of the Caño Palma during flood conditions ten days after its initial capture and marking.

That the frog had crossed the canal by swimming seems likely as the width of the canal in both directions was greater than 10m at most points for at least a passage of 100m north and south of the sites of observation. Ten metres is a long jump for any anuran frog and *Smilisca baudinii* is not known to glide (Savage 2002).

Speculatively, if the frog had leaped from the very top crown of the highest riparian foliage it may have reached the canal side but this remains debatable. Whether the frog left its initial forest residency in response to being marked is debatable, although unlikely, given that the toe-tipping method used on this species is known to not cause adverse affects to amphibians (Kinkead *et al.* 2006).

Recently there has been new evidence from phylogenetic research investigating relationships between amphibian populations separated by boundaries like canals, rivers and oceans. The work deduced that dispersal by frogs of the genus *Eleutherodactylus* (which at time of publication included species known as *Craugastor*) by transient aquatic carrying may have contributed to the huge species diversity of the genus (Kaiser 2002; Savage 2002; Crawford 2003; Heinicke *et al.* 2007).

The observations of *Oophaga pumilio* in this study support part of this hypothesis in that coastal frogs dispersed by either forced mechanisms (like flooding) or by accidental dispersal may be dragged by tide flow out to sea and onto oceanic pathways. Provided such individuals survive the journey there is every chance that mats of vegetation carrying them could be washed up on new islands or countries. There has also been evidence to suggest that some island populations of reptiles may also have been directly affected by this style of transient relocation (Vidal *et al.* 2008).

5.2.5.2 Effects of Predation on Amphibians during Flooding

Where high river level is combined with extensive lateral overspill, as in tropical floodplain areas like Caño Palma, a cycle in which greater opportunities for predators at the higher water levels develops (Junk 1997). This has been documented for numerous species of fish in neotropical floodplains (Welcomme 1979; Meffe 1984; Lowe-McConnell 1987; Junk 1997; Drago *et al.* 2003; Goch *et al.* 2005).

There are many fish species that respond to the explosive increase in food supply fuelled by both flooding of terrestrial land and increasing nutrient supply to the aquatic ecosystem that can rejuvenate water systems post flooding. This is often reflected in growth rates for fish post flood (Goulding 1980; Talling & Lemoalle 1998). Predation by fish subsequently becomes more intense during, and after, flooding with reciprocal advantages and disadvantages for both predator and prey (Goulding 1980; Meffe 1984).

Some fish are known for their predatory habits on amphibians and can negatively influence amphibian populations and their community dynamics through predation and indirect effects (Sih 1992; Stebbins & Cohen 1995; Kats & Ferrer 2003), especially in tropical environments (Heyer *et al.* 1975).

Direct effects of predatory fish on amphibians mostly arise from consumption of adult and larvae (Hecnar & M'Closkey 1997; Kiesecker & Blaustein 1998; Smith *et al.* 1999), and influence the behaviour or performance of adult and larvae (Skelly 1992; Anholt *et al.* 1996; Kiesecker & Blaustein 1998), which subsequently effects their abundance and population dynamics (Sih 1992; Brönmark & Edenham 1994; Skelly 1996).

Indirect effects are a result of interactions between predator and prey or between a resource that may result in a syntopic or competitive outcome for an affected species (Kerfoot & Sih 1987; Lima & Dill 1990; Morin 1999). Indirect effects on amphibians have been studied further more recently and studies have detailed a variety of effects including; changes in microhabitat use (Semlitsch & Reyer 1992; Binckley & Resetarits 2003), changes in timing of diurnal and nocturnal activity

patterns (Skelly & Werner 1990; Semlitsch & Reyer 1992), developmental plasticity in morphological development of larvae (Werner 1986; Van Buskirk *et al.* 1997; Lardner 2000), and a variety of life history ‘costs’ (Ball & Baker 1996), for example; altering breeding phenology in adult amphibians (Kats & Ferrer 2003), induction of early hatching of eggs (Warkentin 1995; Chivers *et al.* 2001), and alteration of community dynamics (Fauth 1990; Lardner 2000; Vredenberg 2004).

The effects of predation by fish can also act in synergy with the impacts of other aquatic predators such as crayfish and insect larvae inducing a double edged affect that often results in further pressures and increased likelihood of declines (Kiesecker & Blaustein 1998). The amphibian responses to fish vary markedly ranging from chemical cue decisions to not enter water with fish resident to developmental strategies and toxicity that make them unpalatable (Kats *et al.* 1988; Duellman & Trueb 1986; Rundio & Olson 2003; Bosch *et al.* 2006; Wells 2007).

Predatory fish were present in the Biological Station pond before, during and after flooding events. They were identified as; *Archocentrus nigrofasciatus* and *Parachromis managuensis* (Cichlidae), *Rhamdia guatemalensis* and *Rhamdia rogersi* (Pimelodidae), and *Astyanax aeneus* (Characidae), and *Atractosteus tropicus* (Lepisosteidae). Many of these fish became trapped in the pond post flooding and remained until the next flood. The size of the fish that became trapped in the pool varied. In most years smaller specimens of the various species (but excluding *Atractosteus tropicus*) were observed.

Whilst present in the Biological Station pond they were observed to feed on and attack eggs and tadpole of breeding amphibians. In particular both Cichlids (*Archocentrus nigrofasciatus* and *Parachromis managuensis*) were prominent predators of *Rana vaillanti* larvae. *Chaunus marinus* larvae were less attacked and tended to survive until metamorphosis. This may be due to the Bufotoxin in their skin which is known for its noxious repelling properties (Jensen & Evans 1934).

After the first flood of 2004/05, a young (<60 cm) *Atractosteus tropicus* was trapped in the Biological Station pond. The fish most likely arrived in the pond during receding waters post flood. *A. tropicus* is an old survivor from prehistoric eras. It is a

voracious and stealthy Garfish that resembles a European pike (*Esox lucius*). It has long vertical needle teeth, a basic mandible and a robust primitive physiology. This species relies on a primitive lung to assist in its oxygen consumption and lunges to the surface of water gulping air (Bussing 1987). It uses a bottom up attack strategy when feeding (Bussing 1987).

Plate 5.2.5.2 Adult *Chaunus marinus* with forelimb injury and healed scar tissue, suspected from predatory fish attack.

The impact the Gar had on smaller fish was instantly observed and the fish was observed to prey on many small cichlids in the pond. Its survival would likely not have lasted due to a limited number of fish present in the pond for it to consume. Nevertheless, its residence in the pond was cut short upon the arrival of a second flood two weeks later. During its short duration of residence the Gar had an impact on breeding adult *Chaunus marinus* that formed part of the population study. Five specimens were observed to receive injuries (Plate 5.2.5.2). Injuries sustained

included lacerations to forearm skin and muscular tissue and complete or partial amputation of the distal end of limbs. All five toads continued to behave normally, but one month after, those observed with limb injuries, exhibited visual signs of weight loss. *Atractosteus tropicus* was the likely cause of the injuries due to its presence in the pond at that time.

To be certain that the specimens were recipients of predator related injuries, all five were collected and euthanized post study, and deposited in the University of Costa Rica amphibian collections. Collection was deemed necessary to discount the possibility that *Ribeiroia* sp. trematodes were not present in specimens. *Ribeiroia* are digenetic trematodes whose lifecycle involves infection of planorbid snails, amphibians and water birds (Johnson & Sutherland 2003). Their occurrence is globally distributed with distinct species being specific to various countries and/or continents (Wilson *et al.* 2005).

Ribeiroia sp. induces limb deformities and extra limb growth in amphibians where metacercariae become lodged between limb joints and phalanges (Johnson *et al.* 1999). *Ribeiroia* are known to cause limb deformities in toads in a manner that looks similar to that which is evident for *Chaunus marinus* at the Biological Station pond (Johnson *et al.* 2001; Blaustein & Johnson 2003; Johnson *et al.* 2003). Whether the injuries sustained by *C. marinus* are a direct result of predation, *Ribeiroia* sp. infection or, as in some species, a synergistic combination (Johnson *et al.* 2006), remains to be investigated.

During flooding a range of other predators took advantage of displaced and vulnerable terrestrial amphibian species. *Caiman crocodilus* (Spectacled Caiman) were observed on numerous occasions taking opportunity of the rising floodwaters by foraging well into (often >100 m) the forest (Grant *et al.* 2008). Caiman are a prominent riparian species along the Caño Palma.

In 2004/05 *Bufo coniferus* continued breeding behaviour during the rising flood in a large congregation in the *Manicaria* zone. This behaviour resulted in the toads becoming a target of predation by caiman which appeared to home in on the concentric water vibrations caused by the toad calling from within water. One young

caiman (50 cm approximately in length) gorged itself on so many *B. coniferus* during this breeding frenzy it became slow in mobility. When disturbed by torchlight it released four dead adult *B. coniferus* from its jaws.

When the floods subsided, caiman sometimes remained in the flood pools. When disturbed, they retreated overland toward the Caño Palma, rapidly slipping in and out of temporary pools (Grant *et al.* 2008). These pools were frequently found to be full of suffocating fish trapped in shrinking pools or anurans utilizing the pools for breeding.

That caiman were feeding on the diverse prey within these seasonally restricted environments seems likely. Fish species present included: *Archocentrus nigrofasciatus* and *Parachromis managuensis* (Cichlidae), *Rhamdia guatemalensis* and *Rhamdia rogersi* (Pimelodidae), and *Astyanax aeneus* (Characidae). *Atractosteus tropicus* (Lepisosteidae) were also hunting in these pools and may also have constituted prey for the caiman.

This observation may imply that caiman periodically abandon their territories within the permanent channel network during flooding to specifically forage for trapped fish within temporary pools in the forest and/or they, along with other fauna, advance into the forest during flooding following the expanding shoreline (Grant *et al.* 2008).

Both *Boa constrictor* and *Corallus annulatus* (Boidae) were observed to lower their perch height and take advantage of opportunities the flooding presented. Although observations were few, on two separate occasions for each species, individual snakes were observed to cross low branches near the water surface, possibly as general mobility or to continue foraging. One sub-adult *Boa constrictor* was observed swallowing a large *Chaunus marinus* during the 2004/05 flood. It would seem plausible from this observation that the snake was taking opportunity of ease of prey capture for the same reasons as caiman and fish. It is not known whether these Boids would feed on amphibian prey on a regular basis because they usually prefer a diet that comprises mammals, bats and birds (Stafford & Henderson 1996).

Tigrisoma mexicanum (Bare-Throated Tiger Heron) were also abundant in forested areas during floods. Herons would awkwardly scramble among low vegetation to drying pools after flooding to capture fish in a similar way to caiman. They did not, however, leave more than 10m from the riparian edge of the Caño Palma. This species was not actively observed hunting but its increased presence in all years at the time of receding floods suggests this species may have increased in numbers to take advantage of food bounties available at this time.

5.3 Experiment 3-Investigation of Flooding, Amphibian Populations and Water Quality Relations

5.3.1 Canonical Correspondence Analysis Results (CCA)

5.3.1.1 Using CCA in ECOM

CCA describes in an objective, data-driven and visual manner, some of the complex patterns in data from field studies, simulations and/or controlled experiments. The results of CCA are usually reported in terms of two lists of eigenvalues (one for X and one for Y) and a canonical correlation graph for each pattern. The largest canonical correlation corresponds to the strongest relation between independent and dependent variables. Subsequent canonical correlations correspond to relations of decreasing strength.

Graphical depictions of canonical correlations are one of the most useful components in a CCA and are helpful when interpreting results. CCA graphs highlight the main patterns in data and provide important deviations within patterns.

On the CCA graphs in ECOM the relative size of correlations is indicated by the relative length of the arrows extending away from the centre (positive correlations) or toward the centre (negative correlations) on the graph. The more horizontal the arrow, the less positive or negative the relationship trend between the variables is. Positively related arrows point upward and negatively related arrows point downward on graphs produced in ECOM.

The individual data points to be compared with trend line arrows are represented by a spot symbol (box or triangle). Where data variable spots are located on the graph depicts the relationship with the trend line arrow. If a data spot is closer to the centre of a graph the relationship is considered weak. The further away from the centre the variable is the stronger the relationship is with the trend. The closer the variable spot is to being in contact with the line the stronger the individual data point is with the exact data value for the trend line arrow.

In ECOM the canonical correlation output considers perfectly correlated output ($R = 1$). Where this anomaly occurs, both series of data responsible cannot be used in the analysis as it will result in a singular matrix (i.e. a 1 is equal to a 1 and thus has no inverse matrix). This can thus lead to an erroneous interpretation of the result. The best analysis will tend to be produced following the selection of variables that are not highly correlated. ECOM graphs plot variables on the ordination axes (or trend line arrows) and allow interpretation of which variables are closely correlated with particular axes. For example, a high positive correlation with an axis will be shown by a variable that has a long arrow pointing in almost the same direction as the axis. A variable with an arrow at almost right angles to an axis indicates that it is almost uncorrelated with the axis.

Transformations used in the CCA involved differing styles of Log transforming data. Data transformation using Log is a mathematical operation that changes the measurement scale of a variable (Osborne 2002). It is usually performed to make a set of data useable with a particular statistical test or method. The question of when, and how, to transform has been debated among statisticians (ter Braak 1995). However, differences in transformations only affect the symmetry of species response curves, not their position along gradients. Therefore, CCA still works well with imperfect transformation (Palmer 1993).

5.3.1.2 Criterion Correction and Results for CCA

For water quality data 2002/03 the CCA results suggested that there was virtually no distinguishing relation between the environmental variables and the negative population trends of *Chaunus marinus* and *Rana vaillanti* ($R < 0.05$, $VIF < 1.5$,

Figures 4.3.1-4.3.4). There was a slight relation between conductivity and the negative linear direction of both *C. marinus* and *R. vaillanti* population trends ($r = 0.57$, $P = 0.08$), but not substantial enough to claim that changing conductivity was responsible for fluctuations in population abundance.

The 2003/04 CCA ordination graph suggested a different relation (Figure 4.3.2). The stronger, positive population trend of *Chaunus marinus* had some suggestion of a weak relationship with all water quality variables. The stable population trend of *Rana vaillanti* also exhibited a slight relation, to fluctuations in oxygen and salinity levels (Figures 4.3.1-4.3.4). However, this relationship is possibly not a strict indication of a relationship between *R. vaillanti* populations and oxygen and salinity levels, but more likely an indication that all of them remain stable through the flooding period.

The 2004/05 CCA plot exhibited a negative population trend for *Chaunus marinus* and a positive trend for *Rana vaillanti* (Figure 4.3.4). *C. marinus* exhibited an indication of a relationship with negative trends of carbon dioxide, but this was again, not especially strong ($r = 0.783$, $P = <0.05$ [Appendix 7.0]). *R. vaillanti* suggested a relationship with salinity but this was also, not substantially strong. The stable population trend of *R. vaillanti* also exhibited a slight relation to fluctuations in oxygen and salinity levels.

Iron and nitrogen data sets were not included in the final analysis as they failed all CCA model criteria by possession of too many zeroes (0). Despite attempts made to log transform this data, no sensible data output was achieved from the test. Even after transforming the raw data using $\text{Log } e(x-1)$ and addition of a single value factor $\text{Log } e + y(x-1)$ the results still failed on persistent similarity (i.e. all results being of the same value; as per nitrate at 0.05mg/l) ($r = 0.783$, $P = <0.05$ [Appendix 7.0]).

5.3.1.3 Interpretation of Successful Data Results for CCA

Results from CCA with population and flooding levels showed that disappearances of species within years of data was relatively low for tenacious species such as *Chaunus marinus* and *Rana vaillanti* (Figures 4.3.1-4.3.4). However, among other

species, especially the forest species such as *Bufo coniferus*, *Craugastor polyptychus*, *Craugastor fitzingeri*, *Craugastor noblei*, *Craugastor persimilis*, *Agalychnis callidryas*, *Dendropsophus phlebodes*, *Hypsiboas rufitelus*, *Scinax elaeochrous*, *Smilisca baudinii* and *Pristimantis diastema*, disappearance was relatively high between years, thus analysis on these species was reduced to dealing each year group separately. Parsimony, the use of the smallest possible number of parameters to model a situation, is essential, so although assumptions about the use of this model for the data could be avoided, by adding further parameters to a model, this inevitably would lead to an increase in the variability of parameter estimates (Cormack & Patil 1979; Begon 1983).

For example; in 2002/03 sampling year period only 13 successful population abundances were completely calculated in Experiment 2. Therefore only the 13 data points for each environmental variable that matched the same day of each population estimate were able to be tested for correlation (see Appendix 7.0 for example of the raw population estimate and environmental variables used in the experiment). This raw data was significantly different in range between environmental variables when compared with population abundance estimates ($r = 0.783$, $P = <0.05$ [Appendix 7.0]).

It is likely that the rise and fall in *Chaunus marinus* population data that relates to the water flooding level rises are mostly due to the simple disappearance of the toads while inundation is present. This does, however, suggest that populations remain stable in a negative or positive direction after flooding conditions, as can be seen in the population estimate graphs (Figures 4.2.1-4.2.8).

5.3.2 Floodplain and Climate Affects on Herpetofauna at Caño Palma

5.3.2.1 Floodplains and Herpetofauna

Due to Caño Palma's unusual hydrological cycle (4.1), finding a site for direct comparison of the influencing factors of floodplain ecology on herpetofauna was difficult and therefore reference has been made to examples of floodplain

herpetology from other geographical regions to help place Caño Palma's herpetology into perspective.

Lowland tropical wet forests had historically been considered aseasonal because of the lack of drastic yearly fluctuations in temperature and humidity. However, long term data is increasingly proving that seasonal rhythms do exist (Leigh *et al.* 1982; McDade *et al.* 1994; Wilson & Sandoval 1996). Within lowland wet forests, neotropical amphibians change seasonally in many aspects of their ecology, including relative abundance (Scott 1976; Toft 1981; Lieberman 1986), age structure within populations (Lieberman 1986; Moreia & Lima 1991; Watling & Donnelly 2002), reproductive phenology (Crump 1974; Watling & Donnelly 2002) and feeding patterns, and diet (Toft 1980; Watling & Donnelly 2002; Whitfield 2005).

Natural hydrological variation in floodplains can affect a range of animals and studies are suggesting that areas with such dynamic water tables may alter the abundance and distribution of amphibians. It can also influence amphibian diversity (Meffe 1984; Donnelly *et al.* 2001a; Huang & Hou 2004; Parris 2004; Mamede & Alho 2006; Rittenhouse & Semlitsch 2007). At Caño Palma the slightly higher ground in the southern part of the property nearest the Biological Station is where higher diversity of herpetofauna was noted. This concurs with Donnelly *et al.* (2001b) observations that areas of terrain that have diverse hydrology with drier and wet patches are more likely to contain more diverse herpetofauna assemblages due to increased terrestrial niches.

Donnelly *et al.* (2001a; 2001b) studied the herpetofauna of the river Kissimmee in central Florida. This arterial river had previously been modified by channel forming processes. The modification resulted in altered hydrology and conversion of floodplain to pasture habitat. Donnelly *et al.* (2001a) documented species presence in five impoundment pools along the river to investigate the conversion effects. They found high concentrations of *Hyla cinerea* and lower proportions of other species. Broadleaved marsh was found to be the most speciose habitat. The Donnelly *et al.* (2001a) study suggested that an increase in abundance of floodplain herpetofauna is likely following the floodplain land reclamation, although if flooding events were to

occur in flash flood years, some species would be prevented from colonising successfully.

In part 2 of the study Donnelly *et al.* (2001b) collected population data using drift fencing and pitfall buckets to capture amphibians. The data from this study indicated that where amphibian species diversity was highest, individuals were trapped in hammocks that adjoined the pasture habitat. Donnelly *et al.* (2001b) also documented patterns of species distribution between pasture and hammock habitats but this data was interrupted by a flood that occurred in conjunction with the 1997-1998 El Niño Southern Oscillation (ENSO).

Hammock features and raised areas of higher ground occur within Caño Palma's forest and although very small in area (often no more than approximately 5m²) and slight in elevation (often no more than 0.5m above the surrounding terrain height) were observed to form the last islands of land available for terrestrial herpetofauna during a flood. This factor, concurrent with Donnelly *et al.* (2001a; 2001b) and Tarkhnishvili & Gokhelaşvili's (1999) observations, is suggestive that many species of amphibian are pooled in population clusters during the flooding event.

Caño Palma's forest experienced a rapid but seasonally predictable shift in its water table that commenced in the early onset of the wetter season. This seasonal shift was similar to that described by Gubányi & Creemers (1994) and Kovács (2002). Gubányi & Creemers (1994) studied species of *Rana* in the Szigetköz floodplain of the river Danube (Hungary), observing distribution and population structure. They took samples and analysed the electrophoretic phenotypes. They concluded that migration within populations was very high causing potentially unstable population structure that was influenced by unpredictable shifts in water table and flooding of riparian pasture habitat. In more recent studies of the same stretches of river, Kovács (2002) reported a total of 12 amphibian (*Rana*, *Triturus*, *Bufo*, and *Bombina* genera) and 3 wetland reptile species (*Natrix* and *Emys* genera) from wetland breeding sites that included oxbow lakes, gravel pits, fishponds, backwaters, Alder Carr swamps and hammock features within wet riparian forest areas.

Kovács (2002) reported that in 2000 the water level did not reach its optimum height, resulting in a maximum success rate for breeding amphibians and optimal growth for aquatic flora. However, in 2001 the flooding returned with a very high water level. The effects of the 2001 flooding are currently being studied.

Also in Europe, Ogielska *et al.* (1998) reported the effect of the irregular flooding of the river Odra, Poland in 1997. They found that some amphibians decreased in numbers from dispersal from metapopulations and that *Hyla arborea* disappeared from parts of its range after the flood. Ogielska *et al.* (1998) also reported that reptile populations remained stable. Borczyk (2001) reported the longer term effects of the same flood on one species of lizard (*Lacerta agilis*). He found that a decrease in numbers of *L. agilis* was noted after the flooding event but that it was not until years after that the population was affected by genetic bottlenecking. This was realised by the many atypically coloured specimens in the population.

The question of whether amphibians at Caño Palma decrease in abundance following or during periods of flooding was investigated in this study and showed that actual abundance did not change significantly, despite species disappearing during flooding and returning after at the site. However, aspects of genetic bottlenecking of the various species as a result of irregular flooding was outside the practical scope of this work but would offer interesting further work.

Richter & Seigel's (2002) studied *Rana sevosa* in the coastal plain forests in southern Mississippi. They found that the population dynamics shifted within years due to lack of recruitment with life expectancy of a population being between 1 and 7 years. Richter & Seigel (2002) concluded that the low rate of return to the breeding site by adults of the population was partially due to the site's geographical isolation. Caño Palma Biological Station is relatively isolated due to its habitats only being connected so far as river boundaries to its south, east and west. However, this isolation may not prevent eventual migration from the area; as demonstrated by *Oophaga pumilio*'s distributional change during flooding and evidence of Gascon *et al.* (1998), who questioned the river barrier hypothesis after showing related populations of frog on either side of a major river.

Tarkhnishvili & Gokhelashvili (1999) studied the spatial structure and population dynamics of *Rana macrocnemis* in riparian and hammock pools, only in the river Nedzura, a tributary of the River MtKvari (known also as the River Kura), in the country of Georgia. They observed frogs spawning in numerous temporary pools and puddles situated along the river bed and concluded that variation in the size of the two populations studied was density-dependant. The regulating force in density-dependency in this case was a loss of juveniles to local habitat sinks that encouraged migration.

At Caño Palma, juvenile dispersal was only observed for two species *Bufo coniferus* and *Chaunus marinus* during this study. In all years *B. coniferus* had bred in part of the area of study during the flood. A flush of newly metamorphosed toadlets was observed in January 2003, January 2004 and February 2005, shortly after flooding had ceased. *C. marinus* was observed to breed at the Biological Station spontaneously throughout the year in all years during this study. Post December flooding of 2003 a small flush of *C. marinus* metamorphs was observed dispersing into Caño Palma forest a week after the flood water had receded. Whether any of these individuals could survive a second flood pulse event (as can occur at Caño Palma) is debatable. However, the observations of young metamorphosed toads prove that at least for *B. coniferus* and *C. marinus* breeding can be successful during flood conditions although it is possible that juvenile dispersal and survival is affected at Caño Palma as for Tarkhnishvili & Gokhelashvili (1999).

That hydroperiod length at Caño Palma influences activity patterns is clearly demonstrated in this study and fits well with hypotheses for other wetland biota that hydroperiod influences and maintains species assemblages (Junk 1997; Baird & Wilby 1999; Junk *et al.* 2000; Ellison 2004a). Arzabe *et al.* (1998) studied calling and activity patterns of 17 species comprising Hylidae, Leptodactylidae and Microhylidae families in lowland Atlantic forest in Sergipe, Brazil. They also observed seasonal reproduction and calling activity that varied according to hydroperiod and rainfall and concluded that hydroperiod length possibly caused control over assemblages and activity patterns at pond habitats.

In a similar study Abrunhosa *et al.* (2006) investigated temporal occupancy of an anuran community in Saquarema near Rio de Janeiro, Brazil. This study revealed that air temperature, pond depth and weather condition were the best predictors to explain amphibian calling activity and behaviour. Temporal analysis also showed anuran succession along different pond gradients of dry, flooded and drying ponds. Multiple regression analysis showed that air temperature, pond depth and weather condition were the best predictors to explain the calling activity in anuran species.

Amphibian communities exhibit strong patterns of temporal variation and breeding success in wetland communities and populations are affected by habitat and environmental factors that interrelate with them (Semlitsch *et al.* 1996; Trenham *et al.* 2003; Werner *et al.* 2007). At Caño Palma different gradients in climate severity were clear. Flooding was more severe and frequent in 2004/05 sample year periods than in 2002/03 and 2003/04 sample year periods. The flooding extended beyond the normal period for seasonal flooding and rainfall was greater. This was reflected in the lower population abundance levels throughout all species during this time. That amphibians at Caño Palma persist along different aquatic gradients in response to the timing of a flooding cycle is possible given the arboreal behaviour demonstrated by some species. This factor may place pressure on those species with weaker response to changes in hydroperiod cycle as for assemblages affected by changes in environmental conditions in the Abrunhosa *et al.* (2006) study.

5.3.2.2 Tropical Climate and Herpetofauna

Among all the environmental factors affecting reproduction and length of the breeding season in tropical anurans, rainfall appears to be the most important abiotic factor (Inger 1969; Crump 1974; Aichinger 1987; Donnelly & Guyer 1994; Bevier 1997; Gottsberger & Gruber 2004), followed by air temperature (Bertoluci 1998; Bertoluci & Rodrigues 2002). Although anuran calling and breeding activities in seasonal tropical sites are intense during the rainy season, differences in the arrival of the species and reproductive phenology are associated with their reproductive mode (Gottsberger & Gruber 2004).

Swanson (1998) examined the relationship that animal populations have with precipitation and presented rates of change in population structure with mammalian and avian examples. He demonstrated that there was a time lag between the effect of precipitation dynamics and actual population fluctuation that would likely have been a result of precipitation influence. The time lag was approximately 1 year before any real noticeable difference in population fluctuation occurred. Swanson (1998) then modelled the data and found that 15 years worth of data could adequately make similar inferences about projected population fluctuation that were not much different to projections from 100 years of data. His study and projections suggested that although animals show temporal autocorrelation, it is not ubiquitous across taxa, and precipitation as an environmental correlate may not always be suggestive of fluctuations.

Such studies on time lags in populations recovering from natural stochastic events is becoming increasingly important in judging the mid and long term turnover of populations in amphibian metacommunities (Marsh & Trenham 2001; Liebhold *et al.* 2004; Werner *et al.* 2007). Whether Caño Palma's amphibian populations would exhibit a time lag response to the flooding that may affect the longer term stability of populations seems possible but would likely require a longer term data sets to decipher details of this factor.

However, short-term climatic events such as heavy rainfall, storms, floods and extended dry season mist frequencies can alter the dynamics of amphibian populations (Pounds 2001). In studies at Monteverde Cloud Forest Biological Station in Costa Rica, drier years in precipitation were correlated with the decline and disappearance of the Golden Toad (*Bufo periglenes*) proving that alterations in climate can place pressure on amphibians due to their physiological limitations (Heatwole 1994; Pounds & Crump 1994; Alford & Richards 1999; Pounds *et al.* 2006).

Also in a study of declines of tropical rainforest frogs in Australia, unusual climate patterns were dismissed as a factor that may have contributed to local amphibian population change (Laurance 1996; Alford & Richards 1999). Laurance's (1996) study relied heavily on predictions of seasonal rainfall and may have undervalued the

variances of heavy aseasonal rainfall acting in synergy with other climate anomalies that may have disrupted natural frog populations. This factor initiated re-examination of the data by Alford & Richards (1999) who highlighted the need for further research into multiple environmental influences that can temporarily disrupt amphibian populations and potentially elucidate an incorrect interpretation of a natural fluctuation, revealing that it is actually a decline trend in an amphibian population.

In a study on the theme of dynamic rainfall and flooding, Cogălniceanu & Miaud (2003) investigated a syntopic species of the urodele genus *Triturus* and the anuran genera *Bombina* and *Rana* on an island called Insula Mică a Brăilei. The island was bounded by a large section of the Danube in Romania. Cogălniceanu & Miaud (2003) investigated life history traits of these amphibians, including population age structure and growth rate as affected by the function of the river floodplain. They discovered that age structure and longevity of the amphibians was affected by the floodplain. Cogălniceanu & Miaud (2003) deduced that flooding in lower stretches of the Danube (including their study area) induced higher mortality rates and reduced longevity in most of the species studied. Longevity of the toad *Bombina bombina* was reduced as much as 6 years compared with other non-flooded sites, indicating that the flooding cycle clearly acted as a stressor by enhancing population turnover and length of time to maturation.

Cogălniceanu & Miaud (2003) suggest that increased mortality risk caused by floodplains acting as stressors could contribute to observed differences in species assemblages between floodplains and river terrace forest.

At Caño Palma the species found are in similar abundance and dominance compared with other lowland tropical sites. This similarity suggests that species are not so heavily influenced in abundance by flooding as a stressor to populations and species may be resistant or adapted to flooding conditions. Conversely species at Caño Palma that were recorded with low abundance are more populous at other lowland tropical wet forest sites. This possibly suggests less flood tolerance by these species.

5.3.2.3 Adaptation by Caño Palma's Herpetofauna to Floodplain the Environment

Due to their semi-aquatic lifecycle amphibians have evolved many diverse specializations to cope with extreme climates, habitats and environments (Duellman & Trueb 1986; Stebbins & Cohen 1995; Pough *et al.* 1998). In floodplains specifically, information regarding any sort of physiological, behavioural or environmental adaptation is sparse and limited to a few studies. This study provides an insight into behavioural adaptation by amphibians in a seasonally flooded forest that has not previously been realised.

At Caño Palma, adaptive behaviour and tolerance was evident from observation where some terrestrial species sought refuge during the flood. However, it is not clear where all terrestrial species went. It is possible that some may have died from drowning if significantly held below waterline for the entire flood duration or could not adequately find suitable refuge. Bosman *et al.* (1997) also reported on the effects of inundation in both an experimental and natural setting for hibernating toads *Bufo bufo* and *Bufo calamita* on the river Rhine, Holland. They concluded that mortality caused under the experimental conditions was high in *B. calamita* but low in *B. bufo* suggesting that the latter species is hardier with a different behavioural response to having its habitat flooded. They reported that *B. bufo* left hibernation steadily after 3-8 days and that *B. calamita* left between 1-6 days, with some individuals of both species returning periodically. They reported that by 30 days 1 *B. bufo* and 14 *B. calamita* died from drowning.

Bosman *et al.* (1997) found that in the natural setting of the river Rhine flooding occurred up to 2.5m above the normal water level and held for up to three weeks depending on the height of the flood. They discovered that *B. bufo* can stand a period of habitat inundation of 25-35 days without leaving its hibernation site. The authors also commented on the clay soils of the river floodplain and noted that complete submersion in the natural settings may not have occurred in some hibernation chambers, thus allowing an extended period of submersion for some individuals.

Annual return to breeding resources was apparent at Cano Palma in several species that were recaptured in multiple years. *Oophaga pumilio*, *Chaunus marinus* and *Rana vaillanti* were all strongly tenacious to reproductive resources. Both female and male *O. pumilio* kept regular watch on territorial tree buttresses where they would likely be guarding bromeliads above. *C. marinus* and *R. vaillanti* returned to the Biological Station pond possibly due to its permanent nature.

Jakob *et al.* (2003) explored breeding phenology and larval distribution in 183 Mediterranean temporary ponds over 3 years in the Roque-Haute nature reserve, southern France. The pools studied were affected by rapid changes in hydrology. They found that species occurrence varied over years and that species with known annual return cycles (e.g. frogs of the genus *Rana* and newts of genus *Triturus*), that regularly return annually to a site with a predictable breeding phenology, were affected by the desiccation and flooding cycle of the pools. Jakob *et al.* (2003) discovered that *Triturus* species exhibited an unusual bimodal phenology, returning to the ponds perhaps twice in a season to breed and to feed prior to a period of aestivation in winter. This kind of adaptive behaviour had not been previously recorded for *Triturus* sp. They also discovered that most larval species preferred deeper temporary pools with a longer hydroperiod

The diet of many species of amphibians is influenced by annual cycles that dictate the abundance and diversity of their prey (Janzen & Schoener 1967; Wolda 1978; Toft 1980; Duellman & Trueb 1986; McDade *et al.* 1994; Stebbins & Cohen 1995). In temperate environments the diversity of prey taxa for amphibians is often lower compared with the tropics (Duellman & Trueb 1986; McDade *et al.* 1994; Stebbins & Cohen 1995; Pough *et al.* 1998; Ortega *et al.* 2005).

Due to this higher diversity of prey types available some tropical amphibians have become generalist predators and some have adapted to specialist dietary preferences (Ortega *et al.* 2005). For example; the toad *Bufo coniferus* and many of the poison dart frogs of the genus *Dendrobates*, *Phylllobates* and *Epipedobates* feed almost exclusively on ants (Toft 1980; 1981; Donnelly 1991; Guyer & Donnelly 2005). Dietary niches could place populations at risk if their selected prey items fall victim

to a stochastic event like a flood that could drown a specialist invertebrate population.

Cogălniceanu *et al.* (2000) studied feeding and dietary preference of amphibians on the Romanian section of the Danube floodplain. They found that amphibian species in the floodplain were mostly non-specialist feeders. Correspondence Analysis revealed that dietary composition overlapped between amphibian species but pressure on the trophic resource was highly partitioned in space and time, allowing for coexistence of large populations of frogs with similar diets.

Hirai (2004) studied diet composition of a single species, *Rana limnocharis*, in ephemeral pools and sand bars in the floodplain habitats of the river Kizu, Japan. Hirai (2004) concluded that *R. limnocharis* had a flexible diet that was found to comprise heavily of Collembolans which were the most abundant arthropods in surveys. It was suggested that this is a useful strategy when coping with feeding during extreme flooding disturbance.

Teixeira *et al.* (2004) produced a similar study to Hirai (2004), only in the Espirito Santo state in southeast Brazil for the anuran *Pseudis bolbodactyla*. Teixeira *et al.* (2004) found that although there was a primary element in the diet (Dipteran larvae) the frog also preyed on a wide diversity of taxa. Both Hirai (2004) and Teixeira *et al.* (2004) describe the ecology of floodplain herpetofauna as ‘understudied’ and ‘largely unknown’.

No formal studies on the dietary composition of amphibian species were completed at Caño Palma and therefore any knowledge relating to such aspects would be anecdotal. However, during the study a dietary note was recorded for *Leptodactylus melanonotus*. A single specimen was found consuming dead tadpoles of *Bufo coniferus* post flood in a desiccated pool (Lewis *et al.* 2008). Whether this act is indicative of the individual frog’s state of hunger following the flood altering normal behaviour remains unanswered.

It is possible that most of the species at Caño Palma feed on a similar prey base as that recorded for them at other sites in the region (Savage 2002; Guyer & Donnelly

2005), although only a minority of species have received quantitative study on their diet. Whether the flood cycle causes a disruption to prey availability is not known.

5.3.2.4 Site Tenacity of Caño Palma's Amphibians

Territoriality and site fidelity are behavioural factors that influence species composition, densities and population regulation (Greenwood 1980; Switzer 1993). Many amphibians exhibit home range sizes ranging from 1-1900m² (Wells 1981; Duellman & Trueb 1986; Sinsch 1990; Blaustein *et al.* 1994b; Pough *et al.* 1998; Wells 2007). Such variability in home range is especially prevalent among amphibians in the tropics where breeding and foraging resources may be monitored and protected by the species that use them (Crump 1986; Roithmair 1994; Pröhl 1997; Wells 2007).

Field experiments of various tropical species illustrate that they are able to home relatively long distances, up to several hundred metres if they are displaced (Crump 1986; Roithmair 1994; Ramirez *et al.* 1998; Tozetti & Toledo 2005). The size of an amphibian's home range can be related to its physiological size both between species and within species (Duellman & Trueb 1986; Ovaska 1992; Wells 2007). Distances moved can also vary depending on age (Breden 1987; Timm *et al.* 2007), sex (Dole & Durant 1974; Ovaska 1992), seasonality (Woolbright 1985), habitat structure (Trenham *et al.* 2001; Rebelo & Helena Leclair 2003) and specialist niche requirements (see Wells 2007).

At Caño Palma, *Oophaga pumilio* exhibited remarkable site fidelity to both territories (for males) and breeding resources (for both males and females). This species is well known for its fidelity to territories and breeding resources at other localities as well (Donnelly 1989c; Pröhl 1997; Haase & Pröhl 2002; Pröhl 2005) and is able to recognize its territory even after 3-6 days isolation in captivity (Baugh & Forester 1994). *Chaunus marinus* and *Rana vaillanti* also exhibited fidelity to breeding resources during the study and these two species are also known for their long distance movements in relation to breeding resources (Carpenter & Gillingham 1987; Ramirez *et al.* 1998).

That these three species were less spatially disoriented by the flooding cycle seems likely as they were often the first species to return to normal wet season breeding behaviour post flooding. They were also the species most likely to be recaptured in all sample year periods. Behavioural fidelity to specific spatial resources has been linked to resource partitioning and maternal habitat resource preference for some species (Toft 1985; Pröhl & Berke 2001; Haase & Pröhl 2002; Rittenhouse & Semlitsch 2007; Wells 2007). With this factor in mind, species at Caño Palma that are more tenacious to breeding resources may exhibit stronger site fidelity than those that are not dependant on a specific niche breeding resource.

For wetland herpetofauna in other global regions, coping with flooding brings about spatial changes and fidelity compromises that would otherwise not readily be shown for particular species (Brown *et al.* 2005). In Australia for example, the snake *Stegonotus cucullatus* (Colubridae) is affected by seasonal inundation on a floodplain in all the home range aspects mentioned above. This disturbance regime forced the otherwise active snake to have a smaller home range compared with specimens found off of floodplain habitat (Brown *et al.* 2005).

5.3.2.5 Diversity and Habitat Structure of Herpetofauna at Caño Palma

Historically, tropical forests outweigh temperate forests in amphibian diversity (Prance 1982; Lugo & Brown 1991; Morely 2000). However, just like temperate forests, tropical forests still change in diversity over gradients of elevation (Fauth *et al.* 1989; Savage 2002) and diversity in habitat composition (Prance 1982; Gentry 1990; Whitmore 1990; Terborgh *et al.* 1996; Laurance & Bierregaard 1997; Goldsmith 1998; Laurance *et al.* 2002).

For tropical wetlands, species diversity has traditionally been considered to be less than that of montane environments and potentially even less in floodplain area forests due to disturbance and habitat dynamics that are radically different within wetland habitats (Duellman 1988; Fauth *et al.* 1989; Myers 1990; Terborgh *et al.* 1996; Duellman 1999; Nebel *et al.* 2001; Savage 2002; Ellison 2004a; Urbina-Cardona *et al.* 2006; Engelbrecht *et al.* 2007).

The lists of species confirmed and observed during this study (Table 1.12.1) combined with species historically observed over 10 years at Caño Palma Biological Station are nearly equal to that of the species count list for the whole of the Tortuguero region (see Appendix 9.0 for Tortuguero Species List). Therefore the notion that *Manicaria* swamp forests are relatively low in diversity of amphibian fauna (Ellison 2004a) may still remain for some environments, but is possibly not so different among lowland forests in similar regions. Comparison of the herpetological assemblages of amphibian species richness of several other documented neotropical wetland sites indicated that swamps actually retain good diversity of amphibian species compared with other lowland forests regionally in Bolivia (Middendorf & Reynolds 2000), Peru (Morales & McDiarmid 1996; Pitman 2006), Brazil (Oliveira-Neckel *et al.* 2000) and Amazonia (Salo *et al.* 1986).

Canopy connectivity and closure can be a determinant in species diversity in wetlands (Skelly *et al.* 2005). Light in relation to specific canopy cover is also shown to influence ground flora, density and diversity as well as the type and species of amphibian drawn to such habitat (Schlaepfer & Gavin 2001; Toral *et al.* 2002). Light levels were notably lower in the rear sections of Caño Palma's forest habitats where *Manicaria saccifera* dominated. Amphibian species distribution in the forest was observed to differ across this habitat gradient. Within the length of transects that bisected all three floral habitats *Oophaga pumilio* was found predominantly in Area A and some of Area B. *Leptodactylus melanonotus* was found predominantly in Area 3 and *Craugastor fitzingeri* found equally in all three zones of the forest.

That the microhabitat differences in the forest were drivers in preference of zone as shown by the three examples is possible. Habitat preference and use is common among nearly all amphibians in both temperate and tropical species of most taxa (for example Gregory 1982; Bertoluci 1998; Chen *et al.* 1999; Watling & Donnelly 2002; Goldberg & Schwalbe 2004; Jenkins *et al.* 2006; Skidde *et al.* 2007). Data on this factor was not analysed as part of this study and thus invites further investigation.

6.0 CONCLUSION

6.1 Aims and Conclusions

The aim for this study was to collect and analyse abundance data for 16 anuran amphibian species at Caño Palma and determine whether flooding caused by the local hydrology, climate and environment influenced local population fluctuation. The study successfully achieved results that supported this aim.

At Caño Palma declines in amphibian numbers and recognition of potential environmental stressors that may be involved had not previously been studied due to a lack of basic data on amphibian abundance in the area. This is a known and common problem in the tropics (1.16). This study successfully collected quantitative amphibian population data for the following 16 anuran amphibian species at Caño Palma Biological Station; *Bufo coniferus*, *Chaunus marinus*, *Craugastor polyptychus*, *Craugastor fitzingeri*, *Craugastor noblei*, *Craugastor persimilis*, *Oophaga pumilio*, *Agalychnis callidryas*, *Dendropsophus phlebodes*, *Hypsiboas rufitelus*, *Scinax elaeochrous*, *Smilisca baudinii*, *Leptodactylus melanonotus*, *Leptodactylus pentadactylus*, *Rana vaillanti* and *Pristimantis diastema* (4.2).

This study was also the first to quantitatively collect/analyse data on the following aquatic environmental stressors that may can affect amphibian populations (see 1.6, 1.16 and 1.17); pH, conductivity, iron, nitrate, hardness, dissolved oxygen, carbon dioxide and salinity.

The study comprised a mark-recapture style (1.21) collection and analysis of abundance data for the 16 anuran species. The study also collected data on local hydrology (1.6) and climate (1.4). The population estimates generated from open population modelling (1.21) were combined with local hydrology, climate and water quality data to elucidate any correlations between amphibian population fluctuation and environmental stressors that may act as precursors to an amphibian population decline (1.16).

The following objectives derived from the study were met;

- The abundance for 14 anuran amphibian species in Caño Palma's forest and 2 species within Caño Palma's was estimated before, during and after flooding events by presence and/or absence via mark-recapture methods (M-RC) and their relation to the rising water table assessed.
- Three years of data were replicated to strengthen the M-RC data and identified fluctuations in population size of the amphibian species over time.
- Some of the movement and re-location patterns of amphibian species were discovered before, during and after the annual flooding period.
- Fluctuations in the local climate cycle were studied and discovered that flooding events are part of the natural hydrological cycle of the area and do disrupting normal metapopulations of amphibians at Caño Palma, but only temporarily.
- Fluctuations in the local climate cycle were successfully studied and relationships between amphibian populations detailed investigating the following climate variables: temperature, humidity, water table levels and water chemistry.
- The differences in the lifecycles of the species studied were described and their ecology discussed in relation to their behaviour during flooding.
- Disruptions to normal breeding behaviour of amphibians during environmental stress were identified to be cessation of breeding during flooding.

Despite successfully completing the above objectives during this study, some components were more successful than others. The climate and hydrological components of the study benefitted from a quantitative, analytical series of experiments that had strategic techniques. They also had concise terminal results to the objectives.

The mark-recapture study for Caño Palma Biological Station's pond clearly exhibited model computation success in the results for both *Chaunus marinus* and *Rana vaillanti*. For forest surveys however, miss-captures were relatively high for

some species such as *Craugastor fitzingeri* (32 captures: and 29 miss-captures in 2003/02; 63:44 - 2003/04; 85:37 – 2004/05; Table 4.2.7). This was possibly due to their fast mobility. Recaptures during this study were therefore reliant on surveyor effort. The methods used (visual encounter survey and leaf-litter quadrat) were also reliant on surveyor effort and this is also a limiting factor to successful results, especially with the low recaptures for some species (e.g. *Craugastor noblei*, *Agalychnis callidryas*, *Dendropsophus phlebodes*, *Hypsiboas rufitelus*, *Scinax elaeochrous* and *Smilisca baudinii*).

Difference in lifecycle, ecology, movement, and behaviour was not possible for all species studied due to their disappearance during flooding. Some species were also so low in local abundance that population modelling and mathematical diagnosis of their population and relating this to flooding was simply not possible. This was a limiting factor that cannot be mitigated for, and a factor that readily becomes apparent in tropical herpetology studies (Savage 2002).

Despite successes with some of the canonical correspondence analysis (CCA) not all water quality variables were able to be successfully computed due to a lack of population data to compare with over time. A larger data set with more results for each species studied may have allowed more substantial analyses.

Despite these limitations the key results from this study were;

- Caño Palma Biological Station's forest is *Manicaria* swamp forest with lowland tropical wet forest on risen hammocks. It is dynamic and unique in that it exists on the boundary of a floodplain and exhibits a biannual, polymodal flooding cycle.
- Temperature, humidity and water chemical composition remained stable in the Caño Palma canal throughout the flooding period with minor fluctuations in salinity indicating pollution was not present in flood waters. The average annual levels of the chemical components studied in Caño Palma are similar to those of other Blackwater canal systems in tropical environments (Furch & Junk 1993; Mertes 1997; Talling & Lemoalle 1998; Lima *et al.* 2003; Ferreira

& Almeida 2005). What was clear from Caño Palma's water quality data over years is that the canal had not been subject to any damaging pollution episodes. Therefore it is possible to conclude that amphibian populations were not likely affected by water chemistry variables during this study.

- Fluctuating abundance of amphibians was correlated with water level changes for all sample year periods. The abundance of the 16 species of anuran amphibian at Caño Palma was affected by the action of flooding, temporarily altering population estimates through time.
- The flooding event caused stress on Caño Palma's amphibians. It temporarily halted seasonal breeding and other normal behaviour patterns in all but a few species. Species reacted in different ways to the flooding event. Some species adapted to the influence of seasonal flooding in Caño Palma's *Manicaria* swamp forest by climbing vegetation. Other species utilised the flood and took the opportunity to breed and continue normal behaviour. Some species suffered increased predation whereas others benefited from a temporary change in resources.
- The flooding event caused temporary disorientation and/or relocation in some species (e.g. *Craugastor fitzingeri* and *Leptodactylus melanonotus*). Other species exhibited strong fidelity to breeding resources or spatial temporal tenacity (e.g. *Oophaga pumilio*, *Rana vaillanti* and *Chaunus marinus*).

In summary, this study successfully completed its objectives for the following species studied; *Chaunus marinus*, *Rana vaillanti*, *Oophaga pumilio* and *Craugastor fitzingeri* but could not successfully conclude the remaining species due to lack of population data. It investigated their ecology and behaviour under conditions of flooding and negated water quality as a factor likely to cause population fluctuation. The study correlated local climate and flooding with populations of the species above and found that they were temporarily stopped from normal breeding activities and forced to adapt in previously unknown ways to torrential flooding conditions.

6.2 Suggestions for Further Study

This study provides the first baseline of amphibian population data to be collected at Caño Palma Biological Station. It serves to stand as a platform for future population work to be compared with. It is hoped that future studies may extend the work already performed herein to monitor the unique and possibly threatened amphibian fauna at Caño Palma Biological Station. With the urgency of amphibian decline ever more present, it is hoped that this study will not be the last of its kind in the Caño Palma region. The following are suggested studies to further this project's findings;

- *Investigate microhabitat preferences by anuran species at Caño Palma* - this data could be tied into population data created by mark-recapture work to investigate occupancy and habitat preference.
- *Investigate correlation of prey abundance and availability with seasonal diet in amphibians at Caño Palma* - this data could be added to population data created by mark-recapture work to investigate prey related ecology that may govern microhabitat selection by amphibia.
- *Investigate maturation and long term turnover of amphibians at Caño Palma in relation to annual climate* – this data could be used to decipher the long term survival prospects for amphibia at Caño Palma.
- *Investigate correlates of flooding with the rise and fall of Tortuguero estuary* – this data could be used to investigate whether Caño Palma is unique in its hydrological catchment zone and whether there is a larger net affect of flooding on amphibia.
- *Investigate correlates of flooding with lunar cycling* – this data could be used in conjunction with more extensive hydrological data to investigate whether flooding at Caño Palma is strictly related to heavy precipitation discharge or whether specific moon cycles create tidal patterns that influence the occurrence of flooding.
- *Investigate genetic bottlenecks of amphibians from flood affected sites in the Tortuguero area* – this data could be used to create the first genetic profile of amphibian populations at Caño Palma and investigate their relations with other amphibian populations in the Tortuguero catchment zone.

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APPENDIX

1.0 Detailed List of Plant Species in Caño Palma Zones

1.1 List of the most common plants of the Edge Vegetation Zone

Scientific Name	Family
<i>Aechmea magdalenae</i> (Andre) Andre ex Baker	Bromeliaceae
<i>Allamanda carthartica</i>	Apocynaceae
<i>Apeiba membranacea</i> Spruce ex Benth	Tiliaceae
<i>Calathea</i> ssp.	Marantaceae
<i>Cecropia obtusifolia</i> Bertol	Cecropiaceae
<i>Conostegia</i> ssp.	Melastomataceae
<i>Costus</i> ssp.	Costaceae
<i>Davilla</i> sp.	Dilleniaceae
<i>Guatteria diospyroides</i> Baill.	Annonaceae
<i>Hampea appendiculata</i> (Donn.Sm.) Standl.	Malvaceae
<i>Heliconia</i> ssp.	Heliconiaceae
<i>Miconia</i> sp.	Melastomataceae
<i>Protium</i> sp. (Rose) Engl.	Burseraceae
<i>Psychotria glomerulata</i> (Donn.Sm) Steyem	Rubiaceae
<i>Psychotria grandis</i> Sw	Rubiaceae
<i>Psychotria poeppigiana</i> Mull. Arg.	Rubiaceae
<i>Psychotria saltatrix</i> C.M. Taylor	Rubiaceae
<i>Senna papillosa</i> (Button & Rose) J. S Ir	Fabaceae/Caesalpinoideae
<i>Simarouba amara</i> Aubl.	Simaroubaceae
<i>Spondias mombin</i>	Anacardiaceae
<i>Symphonia globulifera</i> L.f.	Clusiaceae
<i>Vitex</i> sp.*	Verbenaceae
<i>Xilopia frutescens</i> Aubl.	Annonaceae

* Note; *Vitex* sp. was previously only known in lowland areas of southeastern Nicaragua. This presents a known range extension for this species.

1.2 List of the most common plants of the Transitional Vegetation Zone

Scientific Name	Family
<i>Abarema adenophora</i> (Ducke) Bameby	Fabaceae/Mimosoideae
<i>Apeiba membranacea</i> Spruce ex Benth	Tiliaceae
<i>Brosimum</i> sp.	Moraceae
<i>Byrsonima crispa</i> A.Juss	Malpighiaceae
<i>Carapa guianensis</i> Aubl.	Meliaceae
<i>Casearia sylvestris</i> Sw	Flacourtiaceae
<i>Cassipourea elliptica</i> (Sw) Poit.	Rhizophoraceae
<i>Conostegia</i> ssp.	Melastomataceae
<i>Compsonneura sprucei</i> (A.DC.) Warb.	Myristicaceae
<i>Coussapoa villosa</i> Poepp. & Endl.	Cecropiaceae
<i>Crudia acuminata</i> Benth.	Fabaceae/Caesalpinoideae
<i>Cupania largifolia</i> Radik.	Sapindaceae
<i>Dendropanax arboreus</i> (L.) Decne.&Planch	Araliaceae.
<i>Ficus</i> sp.	Moraceae
<i>Garcinia madruno</i> (Kunth) Hammel	Clusiaceae
<i>Grias cauliflora</i> L.	Lecythidaceae
<i>Guatteria diospyroides</i> Baill.	Annonaceae
<i>Gymnanthes riparia</i> (Schltdl)Klotzsch.	Euphorbiaceae
<i>Hirtella triandra</i> Sw.	Chrysobalanaceae
<i>Hirtella tubiflora</i> Cuatrec.	Chrysobalanaceae
<i>Inga</i> sp.	Fabaceae/Mimosoideae
<i>Machaerium</i> sp.	Fabaceae/Papilionoideae
<i>Malouetia guatemalensis</i> (Mull.Arg.) Standl	Apocynaceae
<i>Manicaria saccifera</i> Gaertn	Arecaceae
<i>Meliosma</i> sp.	Sabiaceae
<i>Miconia</i> sp.	Melastomataceae
<i>Pachira aquatica</i> Aubl.	Bombacaceae
<i>Palicourea</i> sp.	Rubiaceae
<i>Pentaclethra macroloba</i> (Willd) Kuntze.	Fabaceae/Mimosoideae
<i>Protium glabrum</i> (Rose) Engl.	Burseraceae

<i>Psychotria glomerulata</i> (Donn.Sm) Steyem	Rubiaceae
<i>Psychotria grandis</i> Sw	Rubiaceae
<i>Psychotria poeppigiana</i> Mull. Arg.	Rubiaceae
<i>Psychotria saltatrix</i> C.M. Taylor	Rubiaceae
<i>Raphia taedigera</i> Mart.	Arecaceae
<i>Simarouba amara</i> Aubl.	Simaroubaceae
<i>Sloanea</i> sp.	Elaeocarpaceae
<i>Spondias mombin</i> L.	Anacardiaceae
<i>Symphonia globulifera</i> L.f.	Clusiaceae
<i>Sterculia recordiana</i> Standl.	Sterculiaceae
<i>Strychnos panamensis</i> Seem.	Loganiaceae
<i>Tococa guianensis</i> Aubl.	Melastomataceae
<i>Trichia</i> sp.	Meliaceae
<i>Vochysia ferruginea</i> Mart.	Vochysiaceae
<i>Xilopia frutescens</i> Aubl.	Annonaceae
<i>Zygia inequalis</i> (Humb. & Bonpl. exWilld.)	Fabaceae/Mimosoideae

1.3 List of the most common plants of the *Manicaria* Vegetation Zone

Scientific Name	Family
<i>Abarema adenophora</i> (Ducke) Bameby	Fabaceae/Mimosoideae
<i>Abarema macradenia</i> (Pittier) Bameby	Fabaceae/Mimosoideae
<i>Calophyllum brasiliense</i> Cambess.	Clusiaceae
<i>Carapa guianensis</i> Aubl.	Meliaceae
<i>Cassipourea elliptica</i> (Sw) Poit.	Rhizophoraceae
<i>Garcinia madruno</i> (Kunth) Hammel	Clusiaceae
<i>Inga</i> sp.	Fabaceae/Mimosoideae
<i>Lacistema aggregatum</i> (Bergius) Rusby	Flacourtiaceae
<i>Malouetia guatemalensis</i> (Mull.Arg.) Standl	Apocynaceae
<i>Manicaria saccifera</i> Gaertn	Arecaceae
<i>Neea</i> sp.	Nyctaginaceae
<i>Ormosia</i> sp.	Fabaceae/Papilionoideae
<i>Prioria copaifera</i> Griseb	Fabaceae/Caesalpinoideae

<i>Psychotria grandis</i> Sw	Rubiaceae
<i>Souroubea</i> sp.	Marcgraviaceae
<i>Symphoma globulifera</i> L.f.	Clusiaceae
<i>Vitex</i> sp.	Verbenaceae
<i>Vochysia ferruginea</i> Mart.	Vochysiaceae
<i>Zygia inequalis</i> (Humb. & Bonpl.)	Fabaceae/Mimosoideae
<i>Zygia latifolia</i>	Fabaceae/Mimosoideae

2.0 Voucher collection made during field work

TAG No.	SPECIES	LIFESTAGE	YEAR	SEX	IDENTIFIED	CONFIRMATION	LOCATION	NOTES
1	<i>Pristimantis diastema</i>	A	2002		Y	TL Field	CP	
2	<i>Craugastor fitzingeri</i>	A	2002		Y	TL Field	CP	
3	<i>Bufo coniferus</i>	J	2002		Y	TL Field	CP	
4	<i>Craugastor polyptychus</i>	A/SA	2003	Female	Y	FB UCR	CP	
5	<i>Hypsiboas rufitelus</i>	A	2002		Y	TL Field	CP	
6	<i>Hypsiboas rufitelus</i>	J	2002		Y	TL Field	CP	
7	<i>Smilisca baudinii</i>	J	2002		Y	TL Field	CP	
8	<i>Dendropsophus phlebodes</i>	A	2003		Y	TL Field	CP	
9	<i>Agalychnis callidryas</i>	A/SA	2003		Y	TL Field	CP	
10	<i>Smilisca phaeota</i>	A	2003		Y	TL Field	CP	
11	<i>Smilisca baudinii</i>	A	2003		Y	TL Field	CP	
12	<i>Bufo coniferus</i>	A	2003		Y	TL Field	CP	
13	<i>Bufo (Chaunus) marinus</i>	J	2003		Y	TL Field	CP	
14	<i>Scinax elaeochrous</i>	A	2003		Y	TL Field	CP	
15	<i>Scinax elaeochrous</i>	A	2003		Y	TL Field	CP	
16	<i>Craugastor persimilis</i>	J	2003	Female	Y	FB UCR	CP	
17	<i>Pristimantis diastema</i>	J/SA	2003		Y	TL Field	CP	
18	<i>Craugastor fitzingeri</i>	J	2003		Y	TL Field	CP	
19	<i>Craugastor polyptychus</i>	J	2003	Male	Y	FB UCR	CP	
20	<i>Craugastor fitzingeri</i>	A	2003		Y	TL Field	CP	
21	<i>Leptodactylus melanonotus</i>	A	2003		Y	TL Field	CP	
22	<i>Leptodactylus melanonotus</i>	A	2003		Y	TL Field	CP	
23	<i>Leptodactylus melanonotus</i>	T	2003		Y	TL Field	CP	
24	<i>Leptodactylus pentadactylus</i>	J/SA	2003		Y	TL Field	CP	
25	<i>Smilisca baudinii</i>	SA	2003		Y	TL Field	CP	
26	<i>Dendropsophus phlebodes</i>	SA	2003		Y	TL Field	CP	
27	<i>Oophaga pumilio</i>	A	2003		Y	TL Field	CP	

28	<i>Oophaga pumilio</i>	A	2003		Y	TL Field	CP	
29	<i>Pristimantis diastema</i>	A	2003		Y	TL Field	CP	
30	<i>Pristimantis diastema</i>	J	2003		Y	TL Field	CP	
31	<i>Craugastor polyptychus</i>	A	2003		N		CP	LB4 Int Yr Cap (re-grown)
32	<i>Craugastor fitzingeri</i>	SA	2003		Y	TL Field	CP	
33	<i>Tlalocohyla loquax</i>	A	2003		Y	TL Field	CP	
34	<i>Hypsiboas rufitelus</i>	SA	2003		Y	TL Field	CP	
35	<i>Craugastor fitzingeri</i>	SA	2003		Y	TL Field	CP	
36	<i>Craugastor fitzingeri</i>	A	2003		Y	TL Field	CP	
37	<i>Pristimantis diastema</i>	J	2003		Y	TL Field	CP	
38	<i>Craugastor persimilis</i>	J	2003		Y	TL Field	CP	
39	<i>Craugastor polyptychus</i>	SA	2003		N		CP	
40	<i>Craugastor polyptychus</i>	SA	2003		N		CP	
41	<i>Craugastor polyptychus</i>	J	2003	Female	Y	FB UCR	CP	
42	<i>Craugastor polyptychus</i>	A	2003	Female	Y	FB UCR	CP	
43	<i>Craugastor polyptychus</i>	A/SA	2003	Female	Y	FB UCR	CP	
44	<i>Oophaga pumilio</i>	J	2003		Y	TL Field	CP	
45	<i>Oophaga pumilio</i>	J	2003		Y	TL Field	CP	
46	<i>Dendropsophus phlebodes</i>	A	2003		Y	TL Field	CP	
47	<i>Pristimantis diastema</i>	A	2003		Y	TL Field	CP	
48	<i>Scinax elaeochrous</i>	A	2003	Female	Y	TL Field	EFP	In amplexus/deposit eggs
49	<i>Scinax elaeochrous</i>	A	2003	Male	Y	TL Field	EFP	In amplexus
50	<i>Agalychnis callidryas</i>	A	2003	Female	Y	TL Field	CP	Unconfirmed sex
51	<i>Smilisca phaeota</i>	A	2003	Female	Y	TL Field	EFP	Unconfirmed sex
52	<i>Craugastor fitzingeri</i>	SA	2003		Y	TL Field	CP	
53	<i>Agalychnis calcarifer</i>	SA	2003		Y	TL Field	CP	
54	<i>Craugastor fitzingeri</i>	J	2003		Y	TL Field	CP	
55	<i>Craugastor fitzingeri</i>	SA	2003		Y	TL Field	CP	
56	<i>Leptodactylus melanonotus</i>	SA	2003		Y	TL Field	CP	

57	<i>Craugastor polyptychus</i>	J	2003		Y	FB UCR	CP	
58	<i>Hypsiboas rufitelus</i>	SA	2004		Y	TL Field	CP	
59	<i>Bufo coniferus</i>	J	2004		Y	TL Field	CP	
60	<i>Pristimantis diastema</i>	SA	2004		Y	TL Field	CP	
61	<i>Leptodactylus melanonotus</i>	J	2004		Y	TL Field	CP	
62	<i>Craugastor polyptychus</i>	J	2004		N		CP	
63	<i>Craugastor fitzingeri</i>	J	2004		Y	TL Field	CP	
64	<i>Hypsiboas rufitelus</i>	J	2004		Y	TL Field	CP	Metamorph Tad SVL 14 (85)
65	<i>Craugastor polyptychus</i>	A	2004	Male	Y	FB UCR	CP	
66	<i>Craugastor polyptychus</i>	A	2004	Male	Y	FB UCR	CP	
KEY								
TL	Todd Lewis							
Field	Identified in Field (later confirm)							
J	Juvenile							
SA	Sub Adult							
A	Adult							
A/SA	Adult or Sub adult							
J/SA	Juvenile or Sub adult							
SVL	Snout Vent Length							
FB UCR	Federico Bolanos UCR Laboratory							
EFP	Permanent pool E. Fernandez							
CP	Caño Palma forest							

3.0 Historical climate data for Caño Palma Biological Station (collated from historical data recorded by local residents and ex-managers of Caño Palma Biological Station)

Sheet1 Chart 18

November 1994, Max & Min Temperatures

Sheet2 Chart 16

Maximum and Minimum temps, May 96

Sheet1 Chart 19

December 1994, Max & Min Temperatures

Page 1

MCRAIN

4.0 Water quality data

4.1 Water quality data recorded during the 2002/03 survey season and flooding cycle. Yellow highlighting indicates period of flooding

Date	pH	Cond.mg/l	Fe.mg/l	N.mg/l	dH.mg/l	DO.mg/l	CO ₂ .mg/l	SAL.mg/l
10/11/2002	6.1	0.1	0	< 0.05	30	7.8	12.6	0.8
12/11/2002	6	0.08	0	< 0.05	30	9	14	0.6
14/11/2002	6	0.06	0	< 0.05	30	9	13.3	0.8
16/11/2002	6	0.08	0	< 0.05	25	6.7	15	1.1
18/11/2002	5.4	0.06	0.02	< 0.05	30	5.1	12.7	0.8
21/11/2002	5.7	0.03	0	< 0.05	25	4.2	11	0.3
23/11/2002	5	0.05	0	< 0.05	30	6.9	12.8	1.2
25/11/2002	6.3	0.07	0	< 0.05	30	8.4	10	0.8
27/11/2002	6.4	0.05	0	< 0.05	30	9.6	12.9	0.8
29/11/2002	6.6	0.06	0.1	< 0.05	25	6	15	0.8
01/12/2002	6.8	0.06	0.1	< 0.05	20	7.8	15	1.2
03/12/2002	5.7	0.14	0.02	< 0.05	20	4.3	15	1.1
04/12/2002	5.7	0.05	0.02	< 0.05	20	5.7	14	1
06/12/2002	6.8	0.05	0.02	< 0.05	20	2.3	13.6	1.3
08/12/2002	5.4	0.08	0.02	< 0.05	25	5.8	35	0.8
10/12/2002	6.5	0.1	0	< 0.05	30	6.4	18.7	0.6
12/12/2002	5.4	0.07	0	< 0.05	25	8.6	19.3	0.8
15/12/2002	5.7	0.08	0	< 0.05	30	7	19	0.8
16/12/2002	5.7	0.05	0	< 0.05	30	7.2	16.5	0.6
18/12/2002	5.9	0.08	0	< 0.05	30	5.6	17	0.7
20/12/2002	6	0.06	0.02	< 0.05	30	7.8	17	0.5
22/12/2002	6.7	0.07	0.02	< 0.05	30	8	14.1	0.8
25/12/2002	6.8	0.06	0.02	< 0.05	30	8.2	12.4	0.8
27/12/2002	6.8	0.04	0.01	< 0.05	30	9	12.3	0.8
29/12/2002	6.8	0.06	0	< 0.05	30	9.7	16.4	0.8
01/01/2003	6.8	0.08	0	< 0.05	30	6.6	10.6	0.5
02/01/2003	6.8	0.09	0	< 0.05	40	6.4	11	0.7

4.2 Water quality data recorded during the 2003/04 survey season and flooding cycle. Yellow highlighting indicates period of flooding

Date	pH	Cond.mg/l	Fe.mg/l	N.mg/l	dH.mg/l	DO.mg/l	CO ₂ .mg/l	SAL.mg/l
08/11/2003	5.4	0.08	0	< 0.05	30	6.7	12	0.8
10/11/2003	6.1	0.1	0	< 0.05	40	8.1	14	0.8
13/11/2003	5.7	0.12	0	< 0.05	40	8	16.1	0.8
15/11/2003	5.7	0.12	0	< 0.05	40	7.5	17.5	0.8
17/11/2003	5.8	0.05	0	< 0.05	40	7	13.5	0.8
19/11/2003	6.1	0.04	0	< 0.05	40	9.5	12	0.8
21/11/2003	6	0.1	0	< 0.05	30	9.9	13.8	1.2
23/11/2003	6	0.1	0	< 0.05	20	5	15	0.9
24/11/2003	6.3	0.1	0	< 0.05	40	4.5	15.7	1.6
26/11/2003	5.9	0.12	0.02	< 0.05	20	6.9	15	1.1
28/11/2003	6	0.08	0	< 0.05	30	5.7	12	1.2
29/11/2003	5.2	0.1	0.02	< 0.05	30	9.4	18	0.8
01/12/2003	6.1	0.02	0	< 0.05	25	10	20	1.6
03/12/2003	5.4	0.04	0.02	< 0.05	40	8.9	15	1.8
04/12/2003	5.3	0.07	0.02	< 0.05	20	5	12.5	1.2
05/12/2003	5.2	0.05	0.02	< 0.05	20	5.7	14	1
07/12/2003	5.2	0.09	0	< 0.05	35	6	10	1
08/12/2003	6.3	0.04	0	< 0.05	30	5.4	21	1
09/12/2003	6.3	0.04	0	< 0.05	35	5	17	1
11/12/2003	6.2	0.04	0	< 0.05	30	9.5	18	1.2
13/12/2003	6	0.06	0	< 0.05	35	9	20	1.6
15/12/2003	5.7	0.04	0	< 0.05	30	7	16	0.9
17/12/2003	6	0.02	0	< 0.05	40	7.5	12	0.9
19/12/2003	6.4	0.05	0	< 0.05	40	5.1	10	0.9
20/12/2003	6.54	0.09	0	< 0.05	35	7.3	12.5	0.8
22/12/2003	6.12	0.04	0	< 0.05	30	8.1	26	0.8
24/12/2003	5.6	0.1	0	< 0.05	40	8	10.3	0.8
26/12/2003	6.3	0.1	0	< 0.05	40	6.8	10.7	0.8
29/12/2003	6.8	0.04	0	< 0.05	40	7	8.5	0.8
02/01/2004	7	0.05	0	< 0.05	40	8.5	13.7	0.8
04/01/2004	6.9	0.06	0	< 0.05	40	4.2	12	0.8

4.3

Water quality data recorded during the 2004/05 survey season and flooding cycle. Yellow highlighting indicates period of flooding

Date	pH	Cond.mg/l	Fe.mg/l	N.mg/l	dH.mg/l	DO.mg/l	CO ₂ .mg/l	SAL.mg/l
27/10/2004	5.8	0.08	0	< 0.05	50	4	15.6	0.25
29/10/2004	6.5	0.07	0	< 0.05	50	5	12.5	0.9
31/10/2004	6	0.06	0	< 0.05	50	6.5	7	0.8
02/11/2004	5.9	0.07	0	< 0.05	50	6	10	0.8
04/11/2004	5.9	0.04	0	< 0.05	50	5.3	8.5	0.8
05/11/2004	6.9	0.04	0	< 0.05	50	4.7	12.5	0.8
06/11/2004	6.6	0.08	0	< 0.05	50	7.5	2.5	0.8
07/11/2004	6.9	0.05	0	< 0.05	50	5.5	12.5	1.2
07/11/2004	6.9	0.07	0	< 0.05	50	5.8	12	1.4
09/11/2004	6.8	0.05	0	< 0.05	50	6	12	1.8
10/11/2004	6.8	0.05	0	< 0.05	50	4	10	1.2
13/11/2004	7	0.04	0.01	< 0.05	40	6.5	9	1.2
13/11/2004	6.9	0.05	0.01	< 0.05	40	5	14.8	1.2
15/11/2004	6.8	0.03	0	< 0.05	40	7.5	18	0.8
17/11/2004	6.5	0.04	0	< 0.05	50	5	12	0.9
19/11/2004	6.9	0.04	0	< 0.05	27	4	15	1
20/11/2004	6.9	0.04	0	< 0.05	40	6	12	0.6
22/11/2004	6.9	0.04	0	< 0.05	27	5	18	1
24/11/2004	6.9	0.06	0	< 0.05	40	5.2	14	1
26/11/2004	7	0.04	0	< 0.05	40	6.2	17.5	1
28/11/2004	6.9	0.06	0	< 0.05	40	5.2	14	1
30/11/2004	7	0.03	0	< 0.05	40	6	15	0.8
02/12/2004	6.8	0.03	0	< 0.05	40	7.5	18	0.8
04/12/2004	6	0.14	0	< 0.05	40	6.5	12.6	1
06/12/2004	5.9	0.04	0	< 0.05	50	5.3	8.5	0.8
08/12/2004	6.8	0.03	0	< 0.05	40	7.5	10	0.8
08/12/2004	6.9	0.05	0	< 0.05	40	4.5	11.4	0.8
09/12/2004	6.7	0.15	0	< 0.05	40	5	15	1
10/12/2004	6	0.14	0	< 0.05	40	6.5	18.5	1
12/12/2004	6.8	0.07	0	< 0.05	40	7.5	15.5	1
13/12/2004	7	0.16	0	< 0.05	40	7.3	9	0.6
16/12/2004	6.3	0.03	0	< 0.05	40	7	7.5	0.6
18/12/2004	7	0.04	0	< 0.05	40	7.6	6	0.2
20/12/2004	7	0.04	0	< 0.05	40	7	5	0.2
23/12/2004	7	0.02	0	< 0.05	40	7	3	0.2
25/12/2004	6.9	0.22	0	< 0.05	40	9	15.5	0.8
27/12/2004	6	0.03	0	< 0.05	40	8.5	7.5	0.6
30/12/2004	7	0.25	0	< 0.05	40	6	10	0.8
01/01/2005	7	0.25	0	< 0.05	40	6.5	12.5	0.8

5.0 Spearman Rank Correlation, PCA and MANOVA

5.1 Spearman Rank Correlation, PCA and MANOVA for Water Quality 2002/03

YEAR 1 (0203) Spearman Correlations: pH RANK_1, Cond RANK_1, Fe RANK_1, dH RANK_1, DO RANK_1, CO2 RANK_1, SAL RANK_1

	pH RANK_1	Cond RANK_1	Fe RANK_1	dH RANK_1	DO RANK_1	CO2 RANK_1	SAL RANK_1
Cond RANK_1	0.007						
	0.971						
Fe RANK_1	0.146	-0.143					
	0.469	0.477					
dH RANK_1	0.251	0.189	-0.452				
	0.206	0.346	0.018				
DO RANK_1	0.315	-0.012	-0.268	0.362			
	0.109	0.953	0.176	0.064			
CO2 RANK_1	-0.360	0.304	0.085	-0.297	-0.006		
	0.065	0.123	0.674	0.133	0.977		
SAL RANK_1	-0.045	-0.049	0.379	-0.563	-0.199	0.024	
	0.824	0.807	0.051	0.002	0.319	0.905	

Cell Contents: Pearson correlation above, P-Value below

Key

YELLOW = Positive correlation between tabulated factors.

YELLOW/RED = Positive correlation between tabulated factors across 3 years.

YEAR 2 (0304) Spearman Correlations: pH RANK_2, Cond RANK_2, Fe RANK_2, dH RANK_2, DO RANK_2, SAL RANK_2

	pH RANK_2	Cond RANK_2	Fe RANK_2	dH RANK_2	DO RANK_2	CO2 RANK_2	SAL RANK_2
Cond RANK_2	-0.271						
	0.155						
Fe RANK_2	-0.516	0.118					
	0.004	0.541					
dH RANK_2	0.321	-0.036	-0.441				
	0.089	0.854	0.017				
DO RANK_2	0.115	-0.159	-0.025	0.123			
	0.553	0.410	0.898	0.526			
CO2 RANK_2	-0.145	-0.139	0.103	-0.384	0.258		
	0.452	0.474	0.595	0.040	0.177		
SAL RANK_2	-0.227	-0.131	0.261	-0.462	-0.105	0.302	
	0.236	0.500	0.172	0.012	0.587	0.111	

Cell Contents: Pearson correlation above, P-Value below

5.2 Spearman Rank Correlation, PCA and MANOVA for Water Quality 2004/05

YEAR 3 (0405) Spearman Correlations: pH RANK_3, Cond RANK_3, Fe RANK_3, dH RANK_3, DO RANK_3

	pH RNK_1	Cond RNK	Fe RNK_1	dH RNK_1	DO RNK_1	CO2 RNK_
Cond RNK	-0.104 0.530					
Fe RNK_1	0.193 0.240	-0.100 0.544				
DH RNK_1	-0.418 0.008	0.128 0.436	-0.081 0.623			
DO RNK_1	0.078 0.637	-0.022 0.895	-0.086 0.602	-0.088 0.593		
CO2 RNK_	0.087 0.599	0.137 0.404	-0.022 0.893	-0.398 0.012	-0.161 0.327	
SAL RNK_	0.089 0.591	0.183 0.264	0.318 0.048	0.003 0.987	-0.423 0.007	0.377 0.018

Cell Contents: Pearson correlation above, P-Value below

Key

YELLOW = Positive correlation between tabulated factors.

YELLOW/RED = Positive correlation between tabulated factors across 3 years.

Spearman Correlations (Pooled Years): pH RANK, Cond RANK, Fe RANK, dH RANK, DO RANK, CO2 RANK, SAL RANK

	pH RNK	Cond RNK	Fe RNK	dH RNK	DO RNK	CO2 RNK
Cond RNK	-0.208 0.043					
Fe RNK	-0.205 0.047	0.057 0.584				
DH RNK	0.359 0.000	-0.106 0.309	-0.476 0.000			
DO RNK	-0.097 0.352	-0.008 0.942	-0.028 0.784	-0.142 0.171		
CO2 RNK	-0.251 0.014	0.130 0.208	0.155 0.134	-0.462 0.000	0.120 0.246	
SAL RNK	-0.072 0.490	0.026 0.799	0.202 0.050	-0.117 0.259	-0.214 0.037	0.251 0.014

Cell Contents: Pearson correlation above, P-Value below

5.3 Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years

Principal Component Analysis: Year, pH, Cond, Fe/mg/l, DH, DO, CO2/mg/l, SAL

Eigen analysis of the Correlation Matrix

Eigen value	2.5311	1.1758	1.0702	0.9781	0.8515	0.6734	0.4675	0.2522
Proportion	0.316	0.147	0.134	0.122	0.106	0.084	0.058	0.032
Cumulative e	0.316	0.463	0.597	0.719	0.826	0.910	0.968	1.000

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Year	0.530	-0.250	-0.116	-0.031	0.083	0.016	0.403	0.688
pH	0.368	-0.080	0.316	0.259	0.502	0.538	-0.374	-0.101
Cond/mg	-0.001	-0.012	-0.568	0.808	0.045	-0.135	-0.041	-0.041
Fe/mg/l	-0.315	-0.193	0.559	0.354	0.309	-0.254	0.513	-0.049
DH/mg/l	0.542	-0.042	-0.141	-0.143	0.066	-0.146	0.391	-0.697
DO	-0.175	0.498	-0.307	-0.253	0.730	-0.085	0.116	0.099
CO2/mg/l	-0.381	-0.320	-0.314	-0.096	-0.003	0.692	0.387	-0.122
SAL	-0.121	-0.736	-0.195	-0.244	0.327	-0.346	-0.342	-0.049

Key **Red** = Results requiring further investigation from initial Spearman Rank Correlation

Factor	Variable
Years	PC1
pH	PC2
Cond/mg	PC3
Fe/mg/l	PC4
DH/mg/l	PC5
DO	PC6
CO2/mg/l	PC7
SAL	PC8

MANOVA General Linear Model: pH, Conductivity, Fe, DH, DO, CO2, SALINITY Vs Season (1, 2, 3).

MANOVA for Seasons 1, 2, 3 s = 2 m = 2.0 n = 42.0

Criterion	Test Statistic	F	DF	P
Wilk's	0.30833	9.840	(14, 172)	0.000
Lawley-Hotelling	1.84349	11.193	(14, 170)	0.000
Pillai's	0.81494	8.547	(14, 174)	0.000
Roy's	1.59242			

EIGEN Analysis for Seasons 1, 2, 3

Eigen value	1.5924	0.2511	0.00000	0.00000	0.00000	0.00000	0.00000
Proportion	0.8638	0.1362	0.00000	0.00000	0.00000	0.00000	0.00000
Cumulative	0.8638	1.0000	1.00000	1.00000	1.00000	1.00000	1.00000

Eigenvector	1	2	3	4	5	6	7
pH	-0.1031	0.1038	-0.009	-0.013	-0.153	-0.051	-0.04666
Cond/mg	-0.2559	0.1191	-2.323	0.164	0.086	0.446	0.13210
Fe/mg/l	0.6739	3.0809	0.861	4.303	-0.034	2.375	4.65920
DH/mg/l	-0.0142	-0.0039	0.001	0.009	0.005	-0.002	0.00572
DO	0.0227	-0.0164	-0.008	-0.004	-0.018	-0.042	0.03926
CO2/mg/l	0.0005	0.0014	0.000	0.021	0.002	-0.012	-0.01124
SAL	-0.0121	-0.2769	0.000	0.000	-0.225	0.143	0.00000

5.4 Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years

Analysis of Variance for pH, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	8.3425	8.3425	4.1712	18.61	0.000
Error	92	20.6234	20.6234	0.2242		
Total	94	28.9658				

Unusual Observations for pH

Obs	pH	Fit	SE Fit	Residual	St Resid
7	5.00000	6.14074	0.09112	-1.14074	-2.46R
55	7.00000	6.00207	0.08792	0.99793	2.15R

R denotes an observation with a large standardized residual.

Analysis of Variance for Cond/mg, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	0.000365	0.000365	0.000183	0.10	0.909
Error	92	0.176435	0.176435	0.001918		
Total	94	0.176800				

Unusual Observations for Cond/mg

Obs	Cond/mg	Fit	SE Fit	Residual	St Resid
87	0.160000	0.072308	0.007012	0.087692	2.03R
92	0.220000	0.072308	0.007012	0.147692	3.42R
94	0.250000	0.072308	0.007012	0.177692	4.11R
95	0.250000	0.072308	0.007012	0.177692	4.11R

Analysis of Variance for Fe/mg/l, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	0.0028981	0.0028981	0.0014490	6.64	0.002
Error	92	0.0200745	0.0200745	0.0002182		
Total	94	0.0229726				

Unusual Observations for Fe/mg/l

Obs	Fe/mg/l	Fit	SE Fit	Residual	St Resid
10	0.100000	0.013704	0.002843	0.086296	5.95R
11	0.100000	0.013704	0.002843	0.086296	5.95R

Analysis of Variance for DH/mg/l, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	3634.4	3634.4	1817.2	50.38	0.000
Error	92	3318.5	3318.5	36.1		
Total	94	6952.9				

Unusual Observations for DH/mg/l

Obs	DH/mg/l	Fit	SE Fit	Residual	St Resid
27	40.0000	27.9630	1.1558	12.0370	2.04R
33	20.0000	33.6207	1.1153	-13.6207	-2.31R
35	20.0000	33.6207	1.1153	-13.6207	-2.31R
40	20.0000	33.6207	1.1153	-13.6207	-2.31R
41	20.0000	33.6207	1.1153	-13.6207	-2.31R
72	27.0000	42.6667	0.9617	-15.6667	-2.64R
74	27.0000	42.6667	0.9617	-15.6667	-2.64R

5.5 Spearman Rank Correlation, PCA and MANOVA for Water Quality All Years

Analysis of Variance for DO, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	22.171	22.171	11.085	4.51	0.014
Error	92	226.321	226.321	2.460		
Total	94	248.492				

Unusual Observations for DO

Obs	DO	Fit	SE Fit	Residual	St Resid
14	2.3000	7.0037	0.3018	-4.7037	-3.06R

Analysis of Variance for CO2/mg/l, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	222.21	222.21	111.10	6.22	0.003
Error	92	1643.67	1643.67	17.87		
Total	94	1865.87				

Unusual Observations for CO2/mg/l

Obs	CO2/mg/l	Fit	SE Fit	Residual	St Resid
15	35.0000	15.0444	0.8135	19.9556	4.81R
51	26.0000	14.7517	0.7849	11.2483	2.71R
63	2.5000	11.7923	0.6768	-9.2923	-2.23R
91	3.0000	11.7923	0.6768	-8.7923	-2.11R

Analysis of Variance for SAL, using Adjusted SS for Tests

Source	DF	Seq SS	Adj SS	Adj MS	F	P
Year	2	0.76021	0.76021	0.38011	4.62	0.012
Error	92	7.56637	7.56637	0.08224		
Total	94	8.32658				

Unusual Observations for SAL

Obs	SAL	Fit	SE Fit	Residual	St Resid
34	1.60000	1.02414	0.05325	0.57586	2.04R
38	1.60000	1.02414	0.05325	0.57586	2.04R
39	1.80000	1.02414	0.05325	0.77586	2.75R
46	1.60000	1.02414	0.05325	0.57586	2.04R
57	0.25000	0.85256	0.04592	-0.60256	-2.13R
66	1.80000	0.85256	0.04592	0.94744	3.35R
89	0.20000	0.85256	0.04592	-0.65256	-2.31R
90	0.20000	0.85256	0.04592	-0.65256	-2.31R
91	0.20000	0.85256	0.04592	-0.65256	-2.31R

6.0 Jolly-Seber Open Population analysis

6.1 Table showing raw Jolly-Seber Open Population analysis for 2002/03 *Chaunus marinus* capture history data (Not. Def. indicates a no model fit).

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			1	Neg.		
2	0	8	Not Def.	Not Def.	0	Not Def.	Not Def.	0
3	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
4	1	13	13	0	1	Neg.	6.5	0.07692
5	0.6667	13	19.5	7.323	1	Neg.	1.5	0.1538
6	0.6667	14	21	7.937	1	Neg.	-6	0.1429
7	1	15	15	0	1	Neg.	0	0.2
8	1	15	15	0	1	Neg.	0	0.2
9	1	15	15	0	1	Neg.	7.5	0.1333
10	0.6667	15	22.5	8.551	1	Neg.	-3.3	0.1333
11	0.8333	16	19.2	2.907	1	Neg.	0.6333	0.3125
12	0.8571	17	19.83	2.462	1	Neg.	4.167	0.3529
13	0.75	18	24	6.325	1	Neg.	-5	0.1667
14	1	19	19	0	1.184	0.3315	-2.38E-07	0.2105
15	1	22.5	22.5	4.437	0.8	1.32E-05	-2.68E-07	0.2222
16	1	18	18	0	1.181	0.3219	-4.77E-07	0.2778
17	1	21.25	21.25	4.155	0.8	8.68E-06	-2.53E-07	0.2353
18	1	17	17	0	1	Neg.	0	0.1176
19	1	17	17	0	1	Neg.	0	0.2941
20	1	17	17	0	1	Neg.	0	0.1176
21	1	17	17	0	1.098	0.2039	4.77E-07	0.1765
22	1	18.67	18.67	2.277	0.8571	1.18E-05	3.86E-07	0.375
23	1	16	16	0	1.875	1.783	0	0.125
24	1	30	30	20.49	0.5	Neg.	0	0.06667

25	1	15	15	0	1	Neg.	0	0.1333
26	1	15	15	0	1	Neg.	3.75	0.3333
27	0.8	15	18.75	3.59	1	Neg.	-2.75	0.2667
28	1	16	16	0	1	Neg.	0	0.125
29	1	16	16	0	1.08	0.1807	2.469	0.0625
30	0.875	17.29	19.76	2.921	0.875	1.32E-05	1	0.405
31	0.875	16	18.29	1.833	1	Neg.	4.381	0.4375
32	0.75	17	22.67	5.938	1.667	0.8547	-7.778	0.1765
33	1	30	30	10.95	0.5	Neg.	0	0.2
34	1	15	15	0	1	Neg.	0	0.1333
35	1	15	15	0	1.244	0.4428	4.77E-07	0.2667
36	1	18.67	18.67	4.776	0	Not Def.	0	0.2143
37	1	Not Def.	0	Not Def.	Not Def.	Not Def.	14.67	Not Def.
38	1	14.67	14.67	3.611	2.182	2.392	-1.65E-06	0.2727
39	1	32	32	25.92	0.25	Neg.	0	0.125
40	1	8	8	0	0	Not Def.	0	0.125
41	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
42	1	14	14	9.165	0	Not Def.	0	0.1429
43	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
44	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
45	1	8	8	4.899	0.5	Neg.	0	0.25
46	1	4	4	0	1.5	1.262	0	0.25
47	1	6	6	3.464				0.3333
48	1							

6.2 Table showing raw Jolly-Seber Open Population analysis for 2003/04 *Chaunus marinus* capture history data (Not. Def. indicates a no model fit).

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			1	Neg.		
2	0	2	Not Def.	Not Def.	1	Not Def.	Not Def.	0
3	1	4	4	0	1	Neg.	4	0.25
4	0.5	4	8	4.899	1	Neg.	7	0.25
5	0.3333	5	15	10.95	1	Neg.	-8	0.2
6	1	7	7	0	1	Neg.	-7	0.2857
7	0	7	Not Def.	Not Def.	1	Not Def.	Not Def.	0
8	1	8	8	0	1	Neg.	0	0.375
9	1	8	8	0	1.375	0.6915	5.5	0.375
10	0.6667	11	16.5	8.811	0.6667	Neg.	1	0.1818
11	0.6667	8	12	4.243	1.156	0.2819	17.33	0.25
12	0.3333	10.4	31.2	17.27	0.8333	Neg.	-26	0.1923
13	0	12	Not Def.	Not Def.	1	Not Def.	Not Def.	0
14	0.5	13	26	11.96	1	Neg.	-11	0.1538
15	1	15	15	0	1	Neg.	15	0.2
16	0.5	15	30	20.49	1.875	1.282	3.75	0.06667
17	0.5	30	60	41.67	0.5	Neg.	-14	0.06667
18	1	16	16	0	1	Neg.	5.333	0.1875
19	0.75	16	21.33	5.551	1.141	0.259	-1.065	0.1875
20	0.8333	19.4	23.28	5.245	0.9804	0.2645	-2.824	0.2577
21	1	20	20	3.873	0.8	1.77E-05	-2.38E-07	0.25
22	1	16	16	0	1	Neg.	0	0.3125
23	1	16	16	0	1.07	0.1464	4.893	0.3125
24	0.7778	17.13	22.02	3.68	0.8889	Neg.	-2.571	0.4088
25	1	17	17	0	1	Neg.	0	0.1176

26	1	17	17	0	1	Neg.	4.25	0.1765
27	0.8	17	21.25	4.155	1	Neg.	-3.25	0.2353
28	1	18	18	0	1.259	0.46	0	0.2222
29	1	22.67	22.67	5.938	1.412	1.325	1.03E-07	0.1765
30	1	32	32	21.91	0.5	Neg.	0	0.0625
31	1	16	16	0	1.271	0.488	6.778	0.125
32	0.75	20.33	27.11	10.34	0.75	Neg.	-4.333	0.1475
33	1	16	16	0	1	Neg.	0	0.125
34	1	16	16	0	1	Neg.	0	0.3125
35	1	16	16	0	1	Neg.	0	0.125
36	1	16	16	0	0	Not Def.	0	0.125
37	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
38	0	Not Def.	Not Def.	Not Def.	14	Not Def.	Not Def.	Not Def.
39	1	14	14	0	1	Neg.	0	0.2857
40	1	14	14	0	1.286	0.4582	2.38E-07	0.1429
41	1	18	18	4.243	1.111	0.5741	3.333	0.3333
42	0.8571	20	23.33	9.236	0.8254	0.4785	15.41	0.3
43	0.5	17.33	34.67	18.78	0	Not Def.	0	0.2308
44	1	Not Def.	0	Not Def.	Not Def.	Not Def.	9	Not Def.
45	1	9	9	6	0.3333	0.1111	-8.94E-08	0.3333
46	1	3	3	0	0	Not Def.	0	1
47	0.6667	Not Def.	0	Not Def.				Not Def.
48	Not Def.							

6.3 Table showing raw Jolly-Seber Open Population analysis for 2004/05 *Chaunus marinus* capture history data (Not. Def. indicates a no model fit)

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			0.7143	Neg.		
2	0.09091	5	55	46.9	1.167	0.2584	-46.67	0.2
3	1	17.5	17.5	3.307	0.8	Neg.	21	0.2857
4	0.4	14	35	17.75	1.329	0.4176	6.204	0.1429
5	0.4286	22.6	52.73	24.93	0.7143	4.87E-06	19.33	0.1327
6	0.3333	19	57	45.3	1	Neg.	-36	0.05263
7	1	21	21	0	1	Neg.	0	0.2381
8	1	21	21	0	1.54	0.7151	8.083	0.2857
9	0.8	32.33	40.42	16.38	0.708	0.1791	42.18	0.1237
10	0.3333	23.6	70.8	41.33	0.8333	1.41E-05	-36	0.08475
11	1	23	23	0	1	Neg.	0	0.1739
12	1	23	23	0	1.522	0.5634	58.33	0.2174
13	0.375	35	93.33	48.39	0.625	Neg.	-25	0.08571
14	0.75	25	33.33	9.027	1	Neg.	-7.333	0.12
15	1	26	26	0	0	Not Def.	0	0.1154
16	1	Not Def.	0	Not Def.	Not Def.	Not Def.	25	Not Def.
17	1	25	25	0	0	Not Def.	0	0.08
18	0	Not Def.	Not Def.	Not Def.	25	Not Def.	Not Def.	Not Def.
19	0	25	Not Def.	Not Def.	1.341	Not Def.	Not Def.	0
20	0.5714	36.2	63.35	24.56	0.7143	Neg.	-3.25	0.1105
21	0.6667	28	42	16.52	1.224	0.3737	7.753	0.07143
22	0.6	35.5	59.17	24.43	1.031	0.3952	-22.34	0.08451
23	1	38.67	38.67	10.57	0.75	1.32E-05	14.5	0.1034
24	0.6667	29	43.5	11.66	1	Neg.	-12.5	0.1379
25	1	31	31	0	1.301	0.5066	13.44	0.129

26	0.75	40.33	53.78	21.25	0.9677	0.3751	-12.04	0.07438
27	1	40	40	10.95	0	Not Def.	0	0.1
28	1	Not Def.	0	Not Def.	Not Def.	Not Def.	63.75	Not Def.
29	0.6667	42.5	63.75	36.14	0.954	0.3774	1.431	0.04706
30	0.6667	41.5	62.25	24.45	0.6667	Neg.	-12.5	0.09639
31	1	29	29	0	1	Neg.	0	0.1034
32	1	29	29	0	1.216	0.3655	8.812	0.1034
33	0.8	35.25	44.06	13.21	0	Not Def.	0	0.1135
34	1	Not Def.	0	Not Def.	Not Def.	Not Def.	57	Not Def.
35	0.6667	38	57	32.24	0.8205	0.2166	-14.77	0.05263
36	1	32	32	5.657	2.625	2.966	0	0.25
37	1	84	84	70.99	0.377	0.1351	31.67	0.04762
38	0.5	31.67	63.33	24.46	1.091	0.6958	-29.09	0.1579
39	1	40	40	18.97	0.9	0.6019	9.54E-07	0.1
40	1	36	36	16.97	0.5	Neg.	0	0.1111
41	1	18	18	0	1.5	0.5559	45	0.2222
42	0.375	27	72	37.01	0.8438	0.3011	-33.75	0.1111
43	1	27	27	6.874	1.778	1.901	-3.58E-07	0.2222
44	1	48	48	37.95	0.3333	Neg.	-4.77E-07	0.0625
45	1	16	16	0	1	Neg.	0	0.0625
46	1	16	16	0	0	Not Def.	0	0.0625
47	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
48	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
49	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
50	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
51	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
52	1	Not Def.	0	Not Def.	Not Def.	Not Def.	27.92	Not Def.
53	0.8	22.33	27.92	11	1.157	1.093	21.7	0.1791
54	0.5	27	54	53.48	1.571	1.845	-40.86	0.03704
55	1	44	44	36.33	0	Not Def.	0	0.09091

56	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
57	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
58	1	10	10	0	1.35	0.7139	-2.38E-07	0.1
59	1	13.5	13.5	4.861	1.259	1.186	17	0.2222
60	0.5	17	34	33.47	0.6667	0.3484	-10.67	0.05882
61	1	12	12	4.243	0.7708	0.2161	6.167	0.25
62	0.6	9.25	15.42	5.584	1.867	1.812	-7.778	0.3243
63	1	21	21	15.87	1.048	1.234	22	0.1429
64	0.5	22	44	43.36	0.5833	0.6304	-4.667	0.09091
65	0.6667	14	21	18.25	0	Not Def.	0	0.1429
66	0.5	Not Def.	0	Not Def.	0	Not Def.	0	Not Def.
67	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
68	Not Def.	Not Def.	Not Def.	Not Def.				Not Def.
69	0.5							

6.4 Table showing raw Jolly-Seber Open Population analysis for 2002/03 *Rana vaillanti* capture history data (Not. Def. indicates a no model fit)

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			0	Not Def.		
2	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
3	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
4	0	3.75	Not Def.	Not Def.	0.9143	Not Def.	Not Def.	0
5	0.6	8	13.33	4.665	2.6	2.752	17.33	0.375
6	0.5	26	52	51.38	0.4286	0.2898	1.714	0.07692
7	0.5	12	24	16.12	0	Not Def.	0	0.1667
8	0	Not Def.	Not Def.	Not Def.	15	Not Def.	Not Def.	Not Def.
9	1	15	15	10.95	0.3333	Neg.	5	0.2
10	0.5	5	10	6.325	0	Not Def.	0	0.2
11	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
12	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
13	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
14	0	5	Not Def.	Not Def.	1	Not Def.	Not Def.	0
15	1	6	6	0	0	Not Def.	0	0.1667
16	0	Not Def.	Not Def.	Not Def.	6	Not Def.	Not Def.	Not Def.
17	1	6	6	0	0	Not Def.	0	0.3333
18	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
19	1	10	10	6.325	0	Not Def.	0	0.2
20	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
21	0.5	5	10	6.325	1	Neg.	-10	0.2
22	0	6	Not Def.	Not Def.	0	Not Def.	Not Def.	0
23	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
24	1	12	12	7.746	0	Not Def.	0	0.1667
25	0	Not Def.	Not Def.	Not Def.	0	Not Def.	Not Def.	Not Def.

26	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
27	0.5	11	22	21.45	0.8333	0.558	1.667	0.09091
28	0.5	10	20	13.27	0	Not Def.	0	0.2
29	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
30	0.5	9	18	9.165	0.7083	0.3646	12.75	0.3333
31	0.3333	8.5	25.5	22.37	0.9524	0.5208	5.714	0.1176
32	0.3333	10	30	26.5	0	Not Def.	0	0.1
33	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
34	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
35	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
36	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
37	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
38	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
39	0	8	Not Def.	Not Def.	1.778	Not Def.	Not Def.	0
40	1	16	16	10.58	0.5469	0.1396	0	0.125
41	1	8.75	8.75	1.281	0.8	Neg.	-1.04E-07	0.5714
42	1	7	7	0	0	Not Def.	0	0.2857
43	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
44	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
45	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
46	1	12	12	8.485	0	Not Def.	0	0.3333
47	1	Not Def.	0	Not Def.				Not Def.
48	1							

6.5 Table showing raw Jolly-Seber Open Population analysis for 2003/04 *Rana vaillanti* capture history data (Not. Def. indicates a no model fit)

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			3	3.464		
2	0	3	Not Def.	Not Def.	0.3333	Not Def.	Not Def.	0
3	0.4	2	5	0	0.4	0.3098	-2	1
4	0	2	Not Def.	Not Def.	0.7083	Not Def.	Not Def.	0
5	0.1667	8.5	51	47.08	0.7593	0.1879	-25.91	0.1176
6	0.8	10.25	12.81	3.24	1.6	1.461	-20.5	0.3902
7	0	18	Not Def.	Not Def.	0.5	Not Def.	Not Def.	0
8	1	10	10	0	1	Neg.	0	0.2
9	1	10	10	0	0	Not Def.	0	0.2
10	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
11	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
12	0	Not Def.	Not Def.	Not Def.	18	Not Def.	Not Def.	Not Def.
13	1	18	18	12	0.5	Neg.	4.5	0.1111
14	0.6667	9	13.5	4.861	0	Not Def.	0	0.2222
15	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
16	0.5	10	20	13.42	0	Not Def.	0	0.1
17	0	Not Def.	Not Def.	Not Def.	12.67	Not Def.	Not Def.	Not Def.
18	0.5	38	76	75.42	0.3625	0.1535	59.45	0.05263
19	0.1667	14.5	87	81.62	0.7692	0.1529	-36.92	0.06897
20	0.5	15	30	8.944	0.9625	0.2575	3.208	0.3333
21	0.6	19.25	32.08	12.8	3.859	4.645	-0.8039	0.1558
22	0.6667	82	123	116.1	0.2143	0.07813	-8.357	0.04878
23	1	18	18	4.243	0.8333	0.2966	5	0.3333
24	0.75	15	20	7.424	1.063	0.5629	4.25	0.2
25	0.6667	17	25.5	14.03	1.222	0.8256	12.83	0.1176

26	0.5	22	44	30.33	0	Not Def.	0	0.09091
27	0	Not Def.	Not Def.	Not Def.	9	Not Def.	Not Def.	Not Def.
28	0.6	18	30	14.53	0.78	0.2477	13	0.1667
29	0.4286	15.6	36.4	16.75	1.059	0.4209	-9.486	0.1923
30	0.7143	20.75	29.05	10.58	0.8059	0.3506	-5.077	0.241
31	1	18.33	18.33	5.709	0.6	Neg.	2.74E-07	0.2727
32	1	11	11	0	0	Not Def.	0	0.1818
33	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
34	0.5	38	76	75.42	0.55	0.4188	13.2	0.05263
35	0.4	22	55	41.98	0	Not Def.	0	0.09091
36	0.75	Not Def.	0	Not Def.	0	Not Def.	0	Not Def.
37	0.2	Not Def.	0	Not Def.	1.5	Not Def.	6	Not Def.
38	1	6	6	0	0	Not Def.	0	0.1667
39	1	Not Def.	0	Not Def.	Not Def.	Not Def.	39	Not Def.
40	0.3333	13	39	44.9	0	Not Def.	0	0.07692
41	0	Not Def.	Not Def.	Not Def.	0	Not Def.	Not Def.	Not Def.
42	0.3333	Not Def.	0	Not Def.	0	Not Def.	0	Not Def.
43	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
44	0	Not Def.	Not Def.	Not Def.	2.5	Not Def.	Not Def.	Not Def.
45	0.5	10	20	19.18	0.25	Neg.	-2	0.2
46	1	3	3	0	1	Neg.	2	1
47	0.6	3	5	0				1
48	1							

6.6 Table showing raw Jolly-Seber Open Population analysis for 2004/05 *Rana vaillanti* capture history data (Not. Def. indicates a no model fit)

Sample	Proportion of recaptures	Marked animals in population	Population estimate	Std. error pop. est.	Survival estimate	Std. error survival	New animals	Probability of capture
1		0			0.5556	0.4057		
2	0	1.667	Not Def.	Not Def.	0.9	Not Def.	Not Def.	0
3	0.3333	6	18	11.49	0.6	0.1966	1.2	0.3333
4	0.5	6	12	5.888	0.9167	0.316	3.667	0.3333
5	0.5	7.333	14.67	7.463	1.107	0.5133	9.595	0.2727
6	0.4	10.33	25.83	15.94	0.675	0.1682	-6.187	0.1935
7	0.8	9	11.25	2.724	0.8667	0.1949	2.631	0.4444
8	0.7	8.667	12.38	1.977	0.7714	0.2262	8.449	0.8077
9	0.5	9	18	7.746	2.417	1.929	188.5	0.3333
10	0.125	29	232	263.9	0.25	Neg.	-49	0.03448
11	1	9	9	0	1.111	0.2684	-4.77E-07	0.3333
12	1	10	10	1.581	0.925	0.2378	6.167	0.5
13	0.6	9.25	15.42	5.584	0.8	1.87E-05	5.667	0.3243
14	0.5	9	18	6	1	Neg.	-6	0.3333
15	1	12	12	0	0	Not Def.	0	0.1667
16	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
17	0.5	23	46	45.48	0	Not Def.	0	0.04348
18	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
19	0.6667	17	25.5	14.03	0	Not Def.	0	0.1176
20	0	Not Def.	Not Def.	Not Def.	5	Not Def.	Not Def.	Not Def.
21	0.75	15	20	7.424	1	0.3644	4	0.2
22	0.6667	16	24	8.746	1.5	1.07	31.5	0.25
23	0.4	27	67.5	51.69	0.8667	0.647	-27.3	0.07407
24	0.8333	26	31.2	17.27	0	Not Def.	0	0.1923
25	0	Not Def.	Not Def.	Not Def.	2.286	Not Def.	Not Def.	Not Def.

26	0.3333	16	48	33.05	0.85	0.5329	-18.13	0.125
27	0.75	17	22.67	12.14	0.6481	0.2597	31.98	0.1765
28	0.25	11.67	46.67	41.25	0.75	2.16E-05	-24	0.08571
29	1	11	11	0	3.455	3.929	38	0.2727
30	0.5	38	76	75.42	0.3667	0.1798	-3.422	0.05263
31	0.6	14.67	24.44	11.64	0.69	0.1831	-2.492	0.2045
32	0.8	11.5	14.38	3.75	5.12	6.138	374.4	0.3478
33	0.1429	64	448	595.5	0.4095	0.2884	-78.36	0.01563
34	0.2727	28.67	105.1	73.93	0.2727	Neg.	-18.67	0.1047
35	1	10	10	0	1.2	0.337	4.8	0.3
36	0.7143	12	16.8	4.515	2.143	1.644	24	0.4167
37	0.5	30	60	41.23	0.7714	0.911	21.21	0.1667
38	0.4	27	67.5	70.82	0.2333	0.08212	-6.417	0.07407
39	0.75	7	9.333	2.981	2	2.036	29.33	0.4286
40	0.3333	16	48	55.32	0.4444	0.235	-9.333	0.0625
41	0.6667	8	12	6.185	0	Not Def.	0	0.25
42	0	Not Def.	Not Def.	Not Def.	10.5	Not Def.	Not Def.	Not Def.
43	0.25	21	84	103.9	0	Not Def.	0	0.04762
44	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
45	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
46	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
47	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
48	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
49	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
50	0	Not Def.	Not Def.	Not Def.	0	Not Def.	Not Def.	Not Def.
51	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
52	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
53	0	Not Def.	Not Def.	Not Def.	10.5	Not Def.	Not Def.	Not Def.
54	0.25	21	84	103.9	0.4375	0.3109	-19.25	0.04762
55	0.6	10.5	17.5	10.36	0.64	0.5258	-3.2	0.2857

56	1	8	8	4.899	0	Not Def.	0	0.25
57	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
58	0	Not Def.	Not Def.	Not Def.	0	Not Def.	Not Def.	Not Def.
59	0.3333	Not Def.	0	Not Def.	1.5	Not Def.	4.5	Not Def.
60	0.6667	3	4.5	1.061	2	1.708	3	0.6667
61	0.6667	8	12	9.95	0.5556	0.3876	13.33	0.25
62	0.25	5	20	19.18	0.875	0.5745	10.5	0.2
63	0.25	7	28	27.28	0	Not Def.	0	0.1429
64	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
65	0.6667	11	16.5	14.11	0	Not Def.	0	0.1818
66	1	Not Def.	0	Not Def.	Not Def.	Not Def.	0	Not Def.
67	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.	Not Def.
68	Not Def.	Not Def.	Not Def.	Not Def.				Not Def.
69	1							

7.0 Raw correlating components for output computation of CCA for *Chaunus marinus* and *Rana vaillanti*

2002/03	2	3	4	5	6	7	8	9	10	11	12	13										
Chaunus 0203	13	19.2	24	22.5	18	17	17	18.67	15	18.75	16	19.76										
Rana 0203	0	0	0	6	0	0	0	0	0	22	20	18										
2003/04	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Chaunus 0304	0	0	8	7	8	12	31.2	26	60	16	23.28	16	16	22.02	17	21.25	22.67	16	16	16	0	18
Rana 0304	0	0	51	0	10	0	0	13.5	0	76	30	123	18	20	44	0	36.4	18.33	0	55	0	0
2004/05	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Chaunus 0405	52.7	21	40.42	23	93.3	33.3	26	25	0	63.3	59.1	38.67	31	40	0	62.2	29	44.06	32	84	63.33	36
Rana 0405	14.67	11.25	18	9	15.42	18	12	46	0	0	24	67.5	0	22.67	11	76	14.38	448	16.8	60	67.5	48
	23	24	25	26	27	28	29	30														
Cont. Chaunus	18	48	16	0	0	54	0	13.5														
Cont. Rana	12	0	0	0	0	84	0	0														

2002/03	2	3	4	5	6	7	8	9	10	11	12	13
pH	5.4	6.6	6.8	5.7	5.7	6.8	5.4	6.5	5.4	5.7	5.7	5.9
Cond.mg/l	0.06	0.06	0.06	0.14	0.05	0.05	0.08	0.1	0.07	0.08	0.05	0.08
Fe.mg/l	0.02	0.1	0.1	0.02	0.02	0.02	0.02	0	0	0	0	0
dH.mg/l	30	25	20	20	20	20	25	30	25	30	30	30
DO.mg/l	5.1	6	7.8	4.3	5.7	2.3	5.8	6.4	8.6	7	7.2	5.6
CO2.mg/l	12.7	15	15	15	14	13.6	35	18.7	19.3	19	16.5	17
SAL.mg/l	0.8	0.8	1.2	1.1	1	1.3	0.8	0.6	0.8	0.8	0.6	0.7

8.0 Successful raw output computation of CCA for *Chaunus marinus* and *Rana vaillanti*

Variance and Eigenvalues		Can. Axis 1	Can. Axis 2	Axis 3	Axis 4	Axis 5	Axis 6	Axis 7	Axis 8
Number of sites (objects) =	12								
Number of species (response variables) =	7								
Number of environmental (explanatory) variables =	2								
Number of canonical axes =	2								
Number of non-canonical axes =	6								
Total variance (inertia) in species data =	0.012								
Sum of canonical Eigen values =	0.0033								
Sum of non-canonical Eigen values =	0.0087								
Canonical Eigen value =		0.0032	0.0002						
% variance explained =		26.3868	1.3423						
Cumulative% variance =		26.3868	27.7291						
Multiple correlation species/environment scores =		0.783	0.4307						
Kendal rank correlation of species/environment scores =		0.5649	0.3817						
Non-canonical Eigen value =				0.0037	0.0028	0.0009	0.0008	0.0004	0
% variance explained =				30.9475	23.1515	7.7254	6.9591	3.1737	0.3137
Cumulative% variance =				30.9475	54.099	61.8244	68.7836	71.9572	72.2709

9.0 Tortuguero Area Herpetofauna list; revised 2009

LOCATION & NO. OF SPECIES FOUND:			
SCIENTIFIC NAME Note: () indicates a synonym	COMMON NAME Note: { } indicates the Spanish name	CAÑO PALMA	TORTUGUERO AREA
Class- REPTILIA	REPTILES	83	88
Order- Testudinata	Turtles	10	10
Family- Cheloniidae	Sea Turtles	3	3
<i>Chelonia mydas</i>	Green Sea Turtle	•	•
<i>Eretmochelys imbricate</i>	Hawksbill Sea Turtle	•	•
<i>Caretta caretta</i>	Loggerhead Sea turtle	•	•
Family- Chelydridae	Snapping Turtles	1	1
<i>Chelydra serpentine</i>	Common Snapping Turtle	•	•
Family- Dermochelyidae	Sea Turtles	1	1
<i>Dermochelys coriacea</i>	Leatherback Sea Turtle	•	•
Family - Emydidae	Pond Turtles	1	1
<i>Trachemys scripta</i>	Ornate or Tropical Slider	•	•
Family- Geoemydidae	Pond Turtles, Box & Water Turtles	2	2
<i>Rhinoclemmys annulata</i>	Brown Land, Brown Wood , Furrowed or Land Turtle	•	•
<i>Rhinoclemmys funereal</i>	Black River Turtle	•	•
Family- Kinosternidae	Mud Turtles	2	2
<i>Kinosternon angustipons</i>	Narrow-bridged, Central American or Yellow-striped Mud Turtle	•	•
<i>Kinosternon leucostomum</i>	White-Lipped Mud Turtle	•	•
Order- Squamata	Squamates		
Suborder- Sauria	Lizards	28	29
Family- Anguidae	Anguid Lizards	1	1
<i>Diploglossus bilobatus</i>	Central American Galliwasp or Leaf-litter Lizard	•	•
Family- Gekkonidae	Geckos	8	8
<i>Gonatodes albogularis</i>	Yellow-Headed or Central American Day Gecko	•	•
<i>Hemidactylus garnotii</i>	Indo-Pacific or House Gecko	•	•
<i>Hemidactylus frenatus</i>	Asiatic or Pacific House Gecko	•	•
<i>Lepidoblepharis xanthostigma</i>	Boat Gecko, Orange-tailed Ground or Litter Gecko	•	•
<i>Sphaerodactylus homolepis</i>	Caribbean Least or Golden Day Gecko	•	•
<i>Sphaerodactylus millepunctatus</i>	Many Spotted or Dwarf Day Gecko	•	•
<i>Sphaerodactylus</i> sp.		•	•
<i>Thecadactylus rapicaudus</i>	Web-footed or Turnip-tailed Gecko	•	•
Family- Corytophanidae	Casquehead Lizards	3	3
<i>Basiliscus plumifrons</i>	Plumed Basilisk, Green Basilisk	•	•
<i>Basiliscus vittatus</i>	Common Brown or Striped Basilisk	•	•
<i>Corytophanes cristatus</i>	Helmeted Basilisk, Iguana or Forest Chameleon	•	•
Family- Iguanidae	Iguanas	1	1
<i>Iguana iguana</i>	Green Iguana	•	•

Family- Polychrotidae	Anoles & Tree Lizards	9	9
<i>Norops biporcatus</i> (<i>Anolis sl.</i>)	Green Tree Anole	•	•
<i>Norops capito</i> (<i>Anolis sl.</i>)	Pug-Headed or Pug-Nosed Anole	•	•
<i>Norops carpenteri</i> (<i>Anolis sl.</i>)	Carpenter Anole	•	•
<i>Norops humilis</i> (<i>Anolis sl.</i>)	Humble, Leaf-litter or Ground Anole	•	•
<i>Norops lemurinus</i> (<i>Anolis sl.</i>)	Lemur Anole, Canopy Anole	•	•
<i>Norops limifrons</i> (<i>Anolis sl.</i>)	Border Anole, Slender Anole	•	•
<i>Norops oxylophus</i> (<i>Anolis sl.</i>)	Stream Anole	•	•
<i>Norops pentaprion</i> (<i>Anolis sl.</i>)	Tree Bark Anole	•	•
<i>Polychrus gutturosus</i>	Tree Lizard, Canopy Lizard	•	•
Family- Teiidae	Macroteiids	1	2
<i>Ameiva festiva</i>	Central American Ameiva or Whiptail, Festive Jungle Runner	•	•
<i>Ameiva quadrilineata</i>	Four-lined Ameiva or Banded Jungle Runner		•
Family- Gymnophthalmidae	Microteiid Lizards	2	2
<i>Gymnophthalmus speciosus</i>	Golden Spectacled Lizard	•	•
<i>Ptychoglossus plicatus</i>	Keeled Leaf-litter Lizard	•	•
Family- Scincidae	Skinks	2	2
<i>Mabuya unimarginata</i>	Bronze-Backed Climbing Skink	•	•
<i>Sphenomorphus cherriei</i>	Striped Litter Skink	•	•
Family- Xantusiidae	Night Lizards	1	1
<i>Lepidophyma flavimaculatum</i>	Yellow-spotted Night Lizard	•	•
Suborder- Serpentes	Snakes	43	47
Family- Boidae	Boas & Pythons	2	2
<i>Boa constrictor</i>	Boa Constrictor	•	•
<i>Corallus annulatus</i>	Annulated Tree Boa	•	•
Family- Colubridae	Harmless & Rear-fanged Snakes	33	37
<i>Chironius grandisquamis</i>			•
<i>Clelia clelia</i>	Musurana	•	•
<i>Coniophanes fissidens</i>	Yellow Bellied Snake or Brown Spotbelly	•	•
<i>Dipsas bicolor</i>	Neotropical Snail-eater, Red-Striped Thirst Snake	•	•
<i>Dipsas articulata</i>	Central American Snail-eater	•	•
<i>Drymarchon corais</i>	Eastern Indigo Snake	•	•
<i>Drymobius margaritiferus</i>	Speckled Racer	•	•
<i>Enulius sclateri</i>	Collared or Sock-headed Snake	•	•
<i>Hydromorphus concolor</i>	Costa Rican/Central American Red-bellied Watersnake	•	•
<i>Imantodes cenchoa</i>	Brown or Common Blunt-headed Tree Snake, Chunk-headed Snake	•	•
<i>Imantodes inornata</i>	Golden, Brown, or Inornate Blunt-headed Treesnake	•	•
<i>Leptodeira annulata</i>	Machete Savane	•	•
<i>Leptodeira septentrionalis</i>	Northern Cat-eyed Snake	•	•
<i>Leptophis ahaetulla</i>	Green or Giant Parrot Snake {Lora}	•	•
<i>Leptophis depressirostris</i>	Green, Satiny, or Golden-eyed Parrot Snake	•	•

<i>Leptophis mexicanus</i>	Mexican Parrot Snake		•
<i>Leptophis nebulosus</i>	Oliver's, Lined, or Yellow-lipped Parrot Snake	•	•
<i>Mastigodryas melanolomus</i>	Salmon-bellied or Neotropical Racer	•	•
<i>Ninia maculata</i>	Spotted Coffee Snake	•	•
<i>Ninia sebae</i>	Red Coffee Snake	•	•
<i>Oxybelis aeneus</i>	Brown or Mexican Vine Snake	•	•
<i>Oxybelis fulgidus</i>	Green Vine Snake	•	•
<i>Pseustes poecilinotus</i>	Bird-eating, Gray Puffing, Chicken, or Northern Bird Snake	•	•
<i>Rhadinea deccorata</i>	Red-bellied or Elegant Litter Snake	•	•
<i>Sibon annulatus</i>	Annulated or Red-ringed Snail-eater, Ringed Thirst Snake	•	•
<i>Sibon nebulatus</i>	Clouded Slug-eater, Common Snail-eater, Clouded Thirst Snake	•	•
<i>Sibon lamari</i>	Lamar's Thirst Snake	•	•
<i>Sibon longifrenis</i>	Drab Snail-eater	•	•
<i>Spilotes pullatus</i>	Tiger Rat Snake, Mica, Oriole	•	•
<i>Tantilla annulatus</i>	Annulated Centipede Snake	•	•
<i>Tantilla schistose</i>	Red Earth Centipede Snake, Collared Crown Snake	•	•
<i>Tantilla supracincta</i>	Banded Centipede Snake		•
<i>Thamnophis marcianus</i>	Chequered Garter Snake		•
<i>Tretanorhynchus nigroluteus</i>	Black Water, Keeled Mangrove, or Orange Bellied Water Snake	•	•
<i>Urotheca euryzona</i>	Halloween Snake, Ringed Glass-tail, False Coral Snake	•	•
<i>Urotheca pachyura</i>	Litter Snake, Costa Rican Glass-tail	•	•
<i>Xenodon rabdocephalus</i>	False Terciopelo, or False Fer-de-Lance	•	•
Family- Elapidae	Coral Snakes & Sea Snakes	3	3
<i>Micrurus alleni alleni</i>	Allen's Coral Snake	•	•
<i>Micrurus multifasciatus hertwigi</i>	Many-banded Coral Snake	•	•
<i>Micrurus nigrocinctus mosquitensis</i>	Costa Rican Coral Snake	•	•
Family- Tropidophiidae	Dwarf Boas	1	1
<i>Ungaliophis panamensis</i>	Banana Boa, Bromeliad Boa, Dwarf Boa	•	•
Family- Viperidae	Adders & Vipers	4	4
<i>Bothriechis schlegelii</i>	Eyelash Viper or Eyelash Palm Pit-viper	•	•
<i>Bothrops asper</i>	Central American Lancehead, Terciopelo, or Fer-de-Lance	•	•
<i>Lachesis stenophrys</i>	Central American Bushmaster	•	•
<i>Porthidium nasutum</i>	Hog-Nosed Pit-viper	•	•
Order- Crocodylia	Crocodylians	2	2
Family- Alligatoridae	Alligators & Caimans	1	1
<i>Caiman crocodilis</i>	Spectacled Caiman	•	•
Family- Crocodylidae	Crocodiles	1	1
<i>Crocodylus acutus</i>	American Crocodile	•	•

Class- AMPHIBIA	AMPHIBIANS	26	37
Order- Gymnophiona	Caecilians	1	1
Family- Caeciliidae	Caecilians	1	1
<i>Gymnopsis multiplicata</i>	Purple Caecilian	•	•
Order- Anura	Frogs & Toads	25	36
Family- Bufonidae	Toads	2	4
<i>Bufo coniferus</i> (<i>Incilius</i> clade)	Green Climbing Toad	•	•
<i>Bufo haematiitius</i> (<i>Rhaebo</i> clade)	Smooth Skinned, or Leaf-litter Toad		•
<i>Bufo melanochlorus</i> (<i>Incilius</i> clade)	Wet forest or Foothill stream Toad		•
<i>Bufo marinus</i> (<i>Rhinella</i> clade)	Cane, Marine or Giant Toad	•	•
Family- Centrolenidae	Glass Frogs	1	3
<i>Centrolene ilex</i>	Ghost or Limon Giant Glass Frog	•	•
<i>Centrolene prosoblepon</i>	Emerald Glass Frog		•
<i>Hyalinobatrachium fleischmanni</i>	Fleischmann's Glass Frog		•
Family- Craugastoridae	Neotropical Leaf-litter Frogs	6	7
<i>Craugastor fitzingeri</i>	Common Rain, Barking, or Fitzinger's Robber Frog	•	•
<i>Craugastor mimus</i>		•	•
<i>Craugastor noblei</i>	Noble's Leaf-litter or Robber Frog	•	•
<i>Craugastor persimilis</i>		•	•
<i>Craugastor polyptychus</i>		•	•
<i>Craugastor ranoides</i>	Rain Frog		•
<i>Craugastor rugulosus</i>	Rugulose Rainfrog	•	•
Family- Dendrobatidae	Poison-dart Frogs	1	2
<i>Dendrobates pumilio</i>	Strawberry Poison-dart Frog, Blue-Jeans Frog	•	•
<i>Phyllobates lugubris</i>	Striped or Lovely Poison Dart-frog		•
Family- Eleutherodactylidae	Neotropical Frogs	1	1
<i>Diasporus</i> (<i>Eleutherodactylus</i>) <i>diastema</i>	Dink Frog, Common Tink Frog	•	•
Family- Hyliidae	New World Treefrogs	11	12
<i>Agalychnis callidryas</i>	Red-eyed Leaf Frog, Red-eyed Treefrog	•	•
<i>Cruziohyla calcarifer</i>	Splendid Leaf Frog, Barred Treefrog		•
<i>Dendropsophus ebraccatus</i>	Painted, Hourglass, Clown, or Harlequin Treefrog	•	•
<i>Dendropsophus phlebodes</i>	Yellow Treefrog	•	•
<i>Hyloscirtus palmeri</i>	Palmer's Treefrog	•	•
<i>Hypsiboas rufitellus</i>	Red-Webbed Treefrog	•	•
<i>Scinax boulengeri</i>	Boulengeri's Treefrog	•	•
<i>Scinax elaeochroa</i>	Olive Treefrog	•	•
<i>Smilisca baudinii</i>	Mexican, Baudin's, or Van Vliet's Treefrog	•	•
<i>Smilisca phaeota</i>	Masked Treefrog	•	•
<i>Smilisca sordida</i>	Drab Treefrog	•	•
<i>Tlalocohyla loquax</i>	Red-Legged Treefrog	•	•

Family- Leptodactylidae	Neotropical Frogs	2	2
<i>Leptodactylus melanonotus</i>	Sabinal or Black-Backed Frog	•	•
<i>Leptodactylus pentadactylus</i>	Smokey Jungle Frog, Central American Bullfrog	•	•
Family- Microhylidae	Microhylid frogs	0	1
<i>Gastrophryne pictiventris</i>	Southern Narrow-mouthed Toad		•
Family- Ranidae	Holarctic & Paleotropic Frogs	1	2
<i>Rana vaillanti</i>	Vaillant's Frog, Tropical Bullfrog	•	•
<i>Rana warszewitschii</i>			•
Family- Strabomantidae	Neotropical Frogs	0	1
<i>Pristimantis ridens</i>	Pygmy Rain Frog		•
TOTAL SPECIES:		108	124

10.0 Environmental Variables Measured for Each Unit - CCA Graph from Grant (2005).

VARIABLE	UNIT OF MEASUREMENT
1. GPS Position	positions recorded using Garmin 12XL satellite receiver
2. Shade	% cover
3. State of Permanency	2 categories: Temporary water (T), Permanent water (P)
4. Site Class	5 categories: Branch (B), Main (M), Pool, Fynbos, Forest
5. Flow Rate	3 categories: Still water (S), Glides (G), Rapids (R)
6. Size of Water Body	3 categories: < 0.5 m, 0.5-1 m, >1 m wide
7. Aquatic Macrophytes	% cover
8. Sedge (<i>Prionium serratum</i>)	% cover
9. Grass	% cover
10. Vegetation	% cover
11. Exposed Rock	% cover
12. Exposed Sand	% cover
13. Lichen	Presence/ Absence
14. Invasive Alien Plants	Presence/ Absence
15. Elevation	metres above sea level (m a.s.l.)
16. Plant Community *	23 categories: 1. Acid sand flat communities, 2. <i>Chondropetalum</i> - <i>Berzelia</i> upper slope hygic Fynbos, 3. <i>Chondropetalum</i> - <i>Restio</i> tussock marsh, 4. <i>Coleonema album</i> short coastal rock Fynbos, 5. <i>Erica</i> - <i>Osmitopsis</i> seepage fynbos & marsh communities, 6. Fynbos on yellow plinthic soils, 7. <i>Hypolaena</i> - <i>Erica</i> tillite tussock, 8. Kloof forest, 9. Lake, 10. Limestone communities, 11. Low dune scrub and strand pioneers, 12. Mesic seaward slope <i>Erica</i> - <i>Restio</i> veld, 13. Mixed lower slope Fynbos, 14. Palmiet estuary, 15. Riverine scrub, 16. Scree forest, 17. <i>Sideroxylon inerme</i> tall dune scrub, 18. Tall shale forest, 19. Xeric & mesic upper slope <i>Erica</i> - <i>Restio</i> veld, 20. Xeric inland flats <i>Erica</i> - <i>Restio</i> veld, 21. Xeric inland lower slope <i>Erica</i> - <i>Restio</i> veld, 22. Xeric seaward slope <i>Erica</i> - <i>Restio</i> veld, 23. unsurveyed areas

11.0 Checklist of Odonata in the Koegelberg Reserve – Species Codes for CCA Plot from Grant (2005).

Checklist of Odonata in the Koegelberg Biosphere Reserve			
Scientific Name	Common Name	Code	Range
Suborder ZYGOPTERA			
Family SYNLESTIDAE			
1. <i>Chlorolestes conspicuus</i> Hagen in Selys, 1862	Conspicuous Malachite	CC	*
2. <i>Chlorolestes umbratus</i> Hagen in Selys, 1862	White Malachite	CU	*
3. <i>Ecchlorolestes peringueyi</i> (Ris, 1921)	Marbled Malachite	EP	*
Family PROTONEURIDAE			
4. <i>Elatoneura frenulata</i> (Hagen in Selys, 1862)	Sooty Threadtail	EF	**
Family COENAGRIONIDAE			
5. <i>Ceriagrion glabrum</i> (Burmeister, 1839)	Commom Pond Damsel	CG	*****
6. <i>Pseudagrion draconis</i> Barnard, 1937	Mountian Sprite	PD	*
7. <i>Pseudagrion furcigerum</i> (Rambur, 1842)	Cape Sprite	PF	*
8. <i>Pseudagrion kersteni</i> (Gerstaecker, 1869)	Kersten's Sprite	PK	*****
9. <i>Ischnura senegalensis</i> (Rambur, 1842)	Marsh Bluetail	IS	*****
10. <i>Africallagma glaucum</i> (Burmeister, 1839)	Swamp Bluet	AG	*****
11. <i>Agriocnemis falcifera falcifera</i> Pinhey, 1952	White-masked Wisp	AF	*
12. <i>Azuragrion nigradorsum</i> (Selys, 1876)	Sailing Bluet	AN	****
Family CHLOROCYPHIDAE			
13. <i>Platycypha fitzsimonsi</i> (Pinhey, 1950)	Boulder Jewel	PFZ	*
Suborder ANISOPTERA			
Family GOMPHIDAE			
14. <i>Ceratogomphus pictus</i> Selys, 1854	Common Thorntail	CP	*****
15. <i>Paragomphus cognatus</i> (Rambur, 1842)	Boulder Hooktail	PC	*****
16. <i>Paragomphus genei</i> (Selys, 1841)	Common Hooktail	PG	****
Family AESHNIDAE			
17. <i>Aeshna minuscula</i> McLachlan, 1896	Friendly Hawker	AM	**
18. <i>Aeshna subpupillata</i> McLachlan, 1896	Stream Hawker	AS	**
19. <i>Anax imperator</i> Leach, 1815	Blue Emperor	AI	*****
20. <i>Anax speratus</i> Hagen, 1867	Orange Emperor	ASP	*****
Family CORDULIDAE			
21. <i>Syncordulia gracilis</i> (Burmeister, 1839)	Yellow Presba	SG	*
22. <i>Syncordulia venator</i> (Barnard, 1933)	Mahogany Presba	SV	*
Family LIBELLULIDAE			
23. <i>Orthetrum abbotti</i> Calvert, 1892	Little Skimmer	OA	***
24. <i>Orthetrum caffrum</i> (Burmeister, 1839)	White-lined Skimmer	OC	*****
25. <i>Orthetrum julia capicola</i> Kimmins, 1957	Julia Skimmer	OJ	*
26. <i>Orthetrum trinacria</i> (Selys, 1841)	Long Skimmer	OT	*****
27. <i>Nesiothemis farinosa</i> (Forster, 1898)	Black-pointed Skimmer	NF	*****
28. <i>Crocothemis erythraea</i> (Brulle, 1832)	Broad Scarlet	CE	*****
29. <i>Crocothemis sanguinolenta</i> (Burmeister, 1839)	Small Scarlet	CS	****
30. <i>Sympetrum fonscolombii</i> (Selys, 1840)	Red-veined Darter	SF	****
31. <i>Trithemis arteriosa</i> (Burmeister, 1839)	Red-veined Dropwing	TA	*****
32. <i>Trithemis dorsalis</i> (Rambur, 1842)	Lakeside Dropwing	TD	*****
33. <i>Trithemis furva</i> Karsch, 1899	Dark Dropwing	TF	*****
34. <i>Trithemis pluvialis</i> Forster, 1906	Rifle Dropwing	TP	***
35. <i>Trithemis stictica</i> (Burmeister, 1839)	Jaunty Dropwing	TS	****
36. <i>Pantala flavescens</i> (Fabricius, 1798)	Wandering Glider	PFL	*****
37. <i>Tramea limbata</i> (Desjardins, 1832)	Voyaging Glider	TL	***
38. <i>Zygonyx natalensis</i> (Martin, 1900)	Scuffed Cascader	ZN	****

12.0 Successful recovery matrices output computation of Jolly-Seber for *Chaunus marinus* 2002/03 (Table 12.1) and *Rana vaillanti* 2002/03 (Table 12.2).

Table 12.1

Sample i	
1	1
2	0 2
3	0 0 3
4	1 1 1 4
5	2 2 2 2 5
6	0 1 1 1 2 6
7	2 2 2 2 2 3 7
8	0 2 2 2 3 3 3 8
9	0 0 0 0 0 1 2 2 9
10	0 0 0 0 0 0 1 2 2 10
11	0 0 0 1 2 2 2 3 4 5 11
12	2 2 2 2 2 2 3 3 3 3 6 12
13	0 0 0 0 0 0 0 0 1 1 2 3 13
14	0 0 0 0 0 0 0 0 0 0 1 3 4 14
15	0 0 0 0 0 0 0 0 0 0 1 2 3 5 15
16	0 1 1 1 1 1 1 1 1 1 1 2 2 5 16
17	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 2 5 17
18	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 18
19	0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 3 5 19
20	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 20
21	0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 3 3 21
22	0 0 0 0 0 0 0 0 0 0 0 2 3 3 3 3 3 3 4 4 7 22
23	0 0 0 0 0 0 0 0 0 0 0 0 2 2 2 2 2 2 2 2 2 23
24	0 2 2 24
25	0 2 2 25
26	1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 3 3 3 3 3 3 4 4 4 5 26
27	0 4 27
28	0 2 28
29	0 1 29
30	0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 3 3 3 4 5 5 6 7 30
31	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 3 3 3 7 31
32	0 1 1 1 1 1 1 1 1 2 3 32
33	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 2 2 2 2 2 2 2 2 2 5 6 33
34	0 1 1 1 1 1 1 1 2 2 2 34
35	0 1 2 2 3 4 4 35
36	0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 3 3 4 36
37	0 1 2 2 37
38	0 1 2 2 3 4 4 38
39	0 1 1 1 1 4 39
40	0 1 1 1 1 1 1 1 1 1 40

409

**Farnborough College of Technology
School of Applied and Health Sciences**

**Environmental Influences on the Population Ecology of Sixteen Anuran
Amphibians in a Seasonally Flooded Neotropical Forest**

By

Todd R. Lewis

2009

ERRATA – Number order or contents; Chapter 2 was omitted from the thesis text deliberately during editing. Number order of the contents is therefore in error. Chapter 3 - 'Methodology' should read as Chapter 2, 'Results' should read as Chapter 3, 'Discussion' should read as Chapter 4, and 'Conclusion' should read as Chapter 5. Relevant chapter sub-headings, figures, tables, and plates should correspond accordingly.