

SITE OCCUPANCY OF ANURANS IN THE ARTHUR R. MARSHALL LOXAHATCHEE
NATIONAL WILDLIFE REFUGE

By

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To my family: Thank you for all your guidance and support throughout the years, and for encouraging me to follow my passion regardless of where it takes me

To Pamela: Thank you for your love, encouragement, and patience over the years

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
ARMI	Amphibian Research and Monitoring Initiative
BICY	Big Cypress National Preserve
CERP	Comprehensive Everglades Restoration Plan
EDEN	Everglades Depth Estimation Network
ENP	Everglades National Park
NAAMP	North American Amphibian Monitoring Protocol
PAO	Proportion of Area Occupied
Refuge	Arthur R. Marshall Loxahatchee National Wildlife Refuge
SFWMD	South Florida Water Management District
VES	Visual Encounter Survey

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Global declines in amphibians over the past few decades have prompted interest in the distribution and abundance of amphibian populations. Reported causes for declines are numerous, but factors related to anthropogenic disturbance top the list. In response to widespread declines the U.S. National Parks Service initiated a national monitoring program to document distribution and status of amphibians in National Parks. Initial inventories were conducted in Everglades National Park, Biscayne National Park, and Big Cypress National Preserve between 2000 and 2003. These surveys provided baseline data on distribution and status of amphibian populations in National Park lands that can be used as an indicator of the ecological response to large-scale restoration activities associated with the Comprehensive Everglades Restoration Plan.

In the present study, utilizing site occupancy models, I expand the scope of Everglades amphibian monitoring to Arthur R. Marshall Loxahatchee National Wildlife Refuge (Refuge), and explore potential factors affecting site occupancy (hydroperiod and exotic treatment history) and detection probabilities. Eight anuran species were documented in the interior of the Refuge, and occupancy of modeled species was high. Low variation in covariate data made it difficult to draw strong conclusions regarding affects of hydroperiod and treatment history. Detection probabilities for two of the species (*Gastrophryne carolinensis* and *Lithobates sphenoccephalus*)

modeled were relatively low, emphasizing importance of incorporating detection probabilities into study design. A comprehensive understanding of current distribution and abundance of anuran populations in the Refuge provides foundation for development of a long term monitoring program that can be used to assess ecological response to future management actions and other potential stressors.

CHAPTER 1 INTRODUCTION

Reports of widespread and rapid declines in amphibian populations have triggered a dramatic increase in amphibian based research in recent years (Cushman 2006 and references therein). Nearly one-third of all known amphibian species in the world are now threatened with extinction (Baillie et al. 2004). In North America, amphibians are considered to be one of the most threatened taxa (Gibbons et al. 2000, Stuart et al. 2004), with many studies pointing to anthropogenic disturbance as the primary cause for declines (Blaustein and Wake 1995, Noss et al. 1997). The effects of habitat loss, alteration, and fragmentation on amphibian populations are of particular concern (Cushman 2006, Stuart et al. 2004), especially in areas with abundant wetland habitat, a warm and humid tropical or sub-tropical climate, and high human populations (Gallant et al. 2007); conditions common to south Florida.

In response to global population declines, studies have suggested that distribution and abundance of amphibian populations be used as an indicator of effects of anthropogenic disturbance on wildlife and ecosystems as a whole (Sheridan and Olson 2003, Welsh and Ollivier 1998). Use of amphibians as indicators of ecosystem health is supported by the fact that amphibians are sensitive to changes in the environment due to unique life history and physiological characteristics (i.e. small body size, reliance on moisture to maintain gas exchange, and use of ephemeral breeding habitats) (Blaustein et al. 1994, Blaustein and Wake 1990). The biphasic lifecycle of many amphibians, requiring both aquatic and terrestrial habitats at different life stages, (Blaustein et al. 1994, Vitt et al. 1990), makes amphibians particularly susceptible to alterations to the landscape (Alford and Richards 1999, Gallant et al. 2007). Amphibians also occupy a mid-level trophic position, acting as both important predators of small invertebrates and as prey for larger species (Whiles et al. 2006). Many amphibians, particularly anurans, can also

be easily detected and identified using standard cost effective sampling protocols, making them ideal candidates for use as indicators of ecosystem health and ecological response to disturbance in monitoring programs (Waddle 2006, Weir and Mossman 2005).

In the United States, efforts to incorporate amphibians into large scale monitoring programs greatly expanded with the creation of the Amphibian Research and Monitoring Initiative (ARMI). Established by the U.S. Geological Survey (USGS), ARMI was designed to document and monitor distribution and abundance of amphibians on Department of Interior (DOI) lands to determine population status and trends, and to identify possible causes of amphibian declines (ARMI, www.armi.usgs.gov/). Since the conception of ARMI in 2000, large scale amphibian monitoring programs have been established across the country (e.g. Bartelt et al. 2011, Mattfeldt et al. 2009, Smith et al. 2006). These efforts have greatly enhanced the rigor of large scale amphibian monitoring programs through development of sampling designs and adoption of new statistical techniques. Specifically, new classes of occupancy models were adopted that address important sources of error brought about by imperfect detection (MacKenzie et al. 2002, 2005), a subject frequently overlooked in past studies (Yoccoz et al. 2001).

Occupancy models developed by MacKenzie et al. (2002) build on closed population capture-recapture methods and explicitly incorporate imperfect detection into the modeling process by assuming a priori that detection is less than 1. This method, which estimates proportion of sites occupied (PAO) as a state variable, requires that each site is revisited on numerous occasions within a season. On each visit to a site, the species of interest is either detected, with probability p , or not detected. Using collective detection histories from all sites,

sampling occasion detection probabilities are estimated as a function of covariates for each species using a maximum likelihood approach.

Beginning in 2000, the methodology developed by ARMI was adopted for use in large scale herpetofauna inventories on National Park Service lands in south Florida (e.g. Everglades National Park - Rice et al. 2004, Big Cypress National Preserve – Rice et al. 2005). Previous efforts to document amphibian and reptile populations in south Florida were either outdated (Duellman and Schwartz 1958), primarily descriptive (Meshaka et al. 2000), or overlooked the importance of imperfect detection (Casler 2005, Dixon 2011). The goals of the Rice et al. (2004, 2005) inventory studies were to generate up to date species lists, estimate occupancy and detection probabilities for each species across the landscape, and develop a protocol that could be used in future monitoring efforts (Rice et al. 2004, 2005). Establishment of a large scale amphibian monitoring protocol in south Florida was particularly important with Congress's approval of the Water Resources Development Act of 2000, which authorized the Comprehensive Everglades Restoration Plan (CERP). Referred to as the world's largest ecosystem restoration effort, the overarching goal of CERP is to restore flow of water through the Everglades by capturing fresh water that currently flows unused to the Atlantic Ocean and Gulf of Mexico through a series of canals and water control structures constructed over the past century (CERP; www.evergladesplan.org). The biological consequences of years of altered hydrology in the Everglades have been dramatic (Davis and Ogden 1994 and Sklar et al. 1998), highlighting the need for both a comprehensive understanding of the current distribution and abundance of amphibian species and an objective method to document ecological response to anthropogenic disturbance and ecosystem restoration.

In the present study, utilizing field sampling methods and statistical techniques common to regional (Rice et al. 2004) and national (ARMI) monitoring protocols, I expand the scope of Everglades amphibian monitoring to the northern extent of the protected Everglades; one of the remaining areas in the Everglades lacking recent baseline amphibian population data. The specific objectives of the study were fivefold: (1) Document anuran species occupying the interior of the Arthur R. Marshall Loxahatchee National Wildlife Refuge, (2) Determine if different sampling methods vary in their ability to detect anurans in the Refuge, (3) Determine if species specific detection probabilities vary in space and time and as a function of sampling occasion environmental covariates, (4) Evaluate the relationship between anuran species occupancy and hydroperiod, and (5) Evaluate the relationship between anuran species occupancy and prior management activity, primarily in the form of exotic species treatment history.

CHAPTER 2 METHODS

Study Area

Field work for this study was conducted in Arthur R. Marshall Loxahatchee National Wildlife Refuge (hereafter Refuge), in Boynton Beach, Florida (Figure 2-1). The Refuge is the northern-most remnant of the protected Everglades wetland ecosystem, and has been managed by the U.S. Fish and Wildlife Service as a unit of the National Wildlife Refuge system since 1951. As with other parts of the Everglades, the Refuge has been impounded and cutoff from the rest of the wetland ecosystem through the construction of canals, levees, and pump systems. A result of this impoundment is an ecosystem with altered hydrology (Richardson et al. 1990). Today the Refuge experiences an extended hydroperiod in some regions due to a ponding effect and a decreased hydroperiod in others (Brandt et al. 2000, Leach et al. 1971, Sklar et al. 1998). The alteration of hydrological parameters across the Refuge has resulted in changes to natural communities over the past century (Brandt et al. 2000, Richardson et al. 1990).

Today the Refuge encompasses 59,646 ha of Everglades ridge and slough habitat. The landscape is a wetland mosaic of sloughs, wet prairies, sawgrass marshes, and tree islands (Loveless 1959, Brandt et al. 2002). Tree islands, and in particular pop-up tree islands, are a unique feature of the Refuge landscape that distinguishes it from other parts of the greater Everglades Ecosystem. Scattered across the entire central portion of the Refuge, pop-up tree islands are small, generally circular tree islands that originated from floating mats of peat. The structure and upland habitat that tree islands provide increases habitat heterogeneity of the Refuge landscape and as a result are important sources of biodiversity (Sklar and Van de Valk 2003). The variety of habitat types across the Refuge landscape vary in their overall structure and species composition, and are directly tied to variations in hydroperiod (Jordan et al. 1996,

Richardson 1990). Sloughs are deep water habitats that are commonly differentiated by the presence of truly aquatic species (*e.g. Nymphaea* sp., *Utricularia* sp.), wet prairies are shallow water habitats distinguished primarily by graminoids (*e.g. Eleocharis* sp., *Rhynchospora* sp.), and tree islands are upland habitats identified by the presence of shrubs and woody vegetation (*e.g. Persea* sp., *Ilex* sp., *Myrica* sp.) (Loveless 1959).

Sampling Design

This study was conducted in the interior of the Refuge that is characterized by tree islands and ridge and slough habitats. This area also corresponds to the Interior Zone used in ongoing water quality sampling at the Refuge; an area that is less impacted by canal water intrusion and other human impacts (Harwell et al. 2008). Study sites were selected across the Refuge landscape using a stratified random design. Two distinct hydroperiod strata (longer and shorter) were chosen based on historic hydroperiod during drought years (2001 and 2007) to ensure that sampling encompassed both ends of the hydroperiod gradient of the Refuge interior.

Hydroperiod was determined using the Everglades Depth Estimation Network (EDEN) (EDEN; <http://sofia.usgs.gov/eden/>). Within each strata thirty points (buffered at 1000m to meet model closure assumption) were randomly selected using Hawth's Tools (Beyer 2004) in ArcGIS®. In addition, 15 spare points were created to be used as back-up sites in the case that a particular point was unusable.

In spring 2010 each of the 60 random points was visited during the day to establish study sites. At each of the random points the nearest pop-up tree island was selected to be used as a study site. Only islands within 200m of the random point were used. If no pop-up tree islands could be found within 200m of the random point then one of the spare random points was used. Once a tree island was selected, a 4m x 40m transect was set up to run from the interior of the tree island into the marsh. Sampling the ecotone that runs from tree islands into the marsh

ensured that sampling captured much of the habitat diversity found in the interior of the Refuge, and also ensured that both highly aquatic and terrestrial species would be included in surveys. Direction of each transect was haphazardly chosen, but was limited to directions that could accommodate a 40m length transect. Each transect was positioned so that 20m were on the tree island and 20m were in the marsh. The mid-point of each transect was positioned at the water line in May 2010 (mean stage from 1-7 station = 16.54 ft), and corresponded to the transitional zone in vegetation from the aquatic more herbaceous species to the upland woody community. Transects were marked using PVC pipes and reflective flagging tape every 5 meters prior to sampling.

Data Collection

Anuran sampling

Anuran sampling was initiated 09 June 2010 and ran until 09 September 2010. Sampling during this period corresponds to the rainy season in south Florida, and coincides with the time of year when anuran detection probabilities are highest in south Florida (Rice et al. 2004, 2005). Each site was sampled three times throughout the rainy season for adult anurans. To avoid breaking assumptions of occupancy modeling or introducing heterogeneity in detection probabilities, sites were resurveyed on different nights and at different times of night than the original survey. The order in which sites were surveyed was chosen at random using clustered groups of neighboring islands, with revisits to each group following the same order as the initial visits.

The primary sampling technique used was standard visual encounter surveys (VES) (Heyer et al. 1994), where the species of all animals observed was recorded. Following the North American Amphibian Monitoring Protocol (NAAMP; <http://www.pwrc.usgs.gov/naamp/>), surveys began 30 minutes after sunset and finished prior to 1 AM. This period coincides with the

most active time period for most amphibians. Each survey was conducted by two experienced field observers (myself and one rotating assistant). Search effort at each transect was area constrained rather than time constrained, however an attempt was made to spend roughly equal time searching each habitat (tree island & marsh) and each site to avoid spending drastically unequal time at different sites. The goal of each survey was to document every species of anuran present at a site.

Prior to each VES and following a 5 minute silent period an anuran call survey was also conducted at each site. During the first 5 minutes at a site all species of anurans heard vocalizing were recorded. All animals heard vocalizing during the 5 minute period were noted, even if it was possible that the animal was located off of the transect. Approximate location (on transect, adjacent to transect (within 50m), distant call) of each animal heard vocalizing was also recorded. Only individuals recorded on the transect or heard adjacent to the transect were considered present at the site for the occupancy analysis.

Environmental covariates

During the time of sampling, environmental data were recorded at each site to be used as covariates of detection. Air temperature, water temperature, wind speed, relative humidity, and barometric pressure were recorded during every sampling occasion. Presence of rain within 12 hour period of each survey and day of year were later added to this list. Vegetation characteristics along each transect were collected for each site following completion of anuran sampling. An interrupted belt transect was used to document general vegetation density at each site. The percent cover of vegetation (using Daubenmire cover classes) was recorded in 1m² plots laid down every five meters along a transect to account for ground cover and general vegetation density. At each point along a transect canopy cover (using a spherical densiometer) was also recorded to account for overhead cover. In the case that two environmental variables

were correlated ($p < 0.05$), only one was chosen for use in analysis. All data were recorded using a PalmOne handheld unit in the field and was hot-linked to a Microsoft Access[®] database following each nights fieldwork.

Hydroperiod

Hydroperiod data for each site were retrieved from EDEN at the conclusion of the field season. The South Florida Water Management District (SFWMD) water year that runs from May 01-April 30 was used to calculate this value. On-the-ground water depths were recorded at all sites along each transect as a way to ground truth EDEN values. Every five meters along the transect (marked with pvc pipes or flagging tape) water depth was recorded to the nearest 1cm using a meter stick. Depth data was collected before, after, and between each sampling period ($n=5$). Correlations between these data and water depth data collected from the nearest water gage as well as EDEN depth output were later compared as a way to corroborate the EDEN output. Because significant differences between EDEN reported depth and on-the-ground recorded depth were found for 12 of 60 sites, the ground surface data used in EDEN had to be corrected for by using an average of all on-the-ground depth data recorded for each site prior to the final hydroperiod calculation.

Treatment history

The Refuge has some of the densest infestations of exotic vegetation in the Everglades ecosystem (Woodmansee et al. 2005). To combat invasion and spread of exotic species the Refuge has enacted an aggressive year-round treatment program, utilizing both manual removal and herbicide application to control dense populations of exotics species such as Old World climbing fern (*Lygodium microphyllum*) and Melaleuca (*Melaleuca quinquenervia*). While the negative effects of herbicides on amphibians have been documented in other studies (Cauble and Wagner 2005, Mann and Bidwell 1999), testing the direct effect of chemicals was not feasible in

this study. Rather, the focus of this research was the timing of management activity (i.e. exotic species contractor activity on and around study sites) and its affect on anuran occupancy. In other words, are sites that were treated or in the vicinity of recently treated areas more likely to lack anuran species than areas not treated in the past three years. Treatment history (date, location) is recorded by Refuge staff on a 1km grid scale. This information was used to determine the most recent treatment date for each grid cell corresponding to a study site from this study.

Data Analysis

Following other anuran surveys in the region (i.e. Rice et al. 2005), the modeling approach adopted for this study was based on the occupancy models developed by MacKenzie et al. (2002, 2005). The software program PRESENCE (Hines 2006) was used to calculate detection and occupancy estimates using the single-species single-season model. Throughout this paper the symbols of ψ and p will be used to represent species occupancy and detection probabilities, respectively.

The first set of analyses conducted evaluate effects of the two different survey methods by assuming that species occupancy and detection probabilities were constant across both space and time [i.e. $\psi(\cdot)$ $p(\cdot)$]. This model is not the best representation of the data, but by holding both occupancy and detection constant for each species relative impacts of each sampling method can be determined without having to worry about unknown biases introduced by models with different covariates (Bailey et al. 2004, Boulinier et al. 1998). Estimates produced from the constant model, along with the proportion of sites where a species was observed [i.e. $\psi(\text{obs})$] were compared across three datasets: (1) call survey data only, (2) VES data only, and (3) the combined dataset.

A two-step process was employed to estimate site occupancy and detection probabilities as a function of covariates for anurans in the Refuge using the combined dataset. In the first step

covariates thought to influence detection probabilities were modeled, including: air temperature, humidity, percent vegetation cover, day of year, and presence of rain within 12 hour period of each survey. From this list an a priori model set was created based on biological knowledge of the species and results from previous research conducted in the region (Appendix A). Additive, interactive, and higher-order terms (e.g. quadratic) were considered in this step. For example, to allow for a peak in detection probability, both a linear (Day) and quadratic (Day+Day²) day of season effect were included. In this first step, occupancy was held constant while modeling which factors best explained detection probabilities [i.e. $\psi(\cdot)p(\text{covariate})$].

In the second step of the modeling process, the best detection model for each species was paired with occupancy variables that represented biological hypotheses (Burnham and Anderson 1998). Two specific occupancy variables were considered: hydroperiod and treatment history. Hydroperiod represents the number of days with standing water at each site during the 2010 SFWMD water year. Treatment history was used as a binary variable; that is, each site was coded as either being treated for exotics in last three years (1) or not treated in the last three years (0). Unfortunately, more detailed treatment history was not available at the time of analysis.

The final model set was kept small by employing the two step approach, with two occupancy variables and a single best detection model per species. Prior to analysis all variables were standardized to avoid problems with parameter estimation in program PRESENCE, and correlated variables ($p < 0.05$) were not included in the same model in order to avoid multicollinearity issues. Models for each species were fit and maximum likelihood estimates were obtained in program PRESENCE and ranked using Akaike's Information Criterion (AIC). The goodness-of-fit of at least one model in each model set was assessed following the methods of MacKenzie and Bailey (2004). All models included factors thought to affect parameter

estimates (ψ, p) and as a result do not represent all possible environmental or biological processes that may influence occupancy or detection probabilities.

CHAPTER 3 RESULTS

Eight anuran species, totaling 812 individuals, were observed at the 60 study sites between 09 June to 09 September, 2010 (Table 3-1). Six species were observed using both VES and call surveys, while *Anaxyrus terrestris* was only observed during VES and *Hyla femoralis* was only recorded during call surveys (Table 3-2). Five of the species observed were either observed too frequently (*Acris gryllus* (naïve occupancy = 100%), *Lithobates grylio* (naïve occupancy = 100%)) or not frequently enough (*Pseudacris ocularis* (naïve occupancy = 1%), *Anaxyrus terrestris* (naïve occupancy = 0.6%), *Hyla femoralis* (naïve occupancy = 2%)) to model. *Acris gryllus* and *Lithobates grylio* were found at every site on nearly every occasion and thus occupy 100% of sites with near perfect detection. *Pseudacris ocularis*, *Anaxyrus terrestris*, and *Hyla femoralis* were only observed on a few nights, and as a result reliable occupancy and detection estimates could not be obtained. The three species that are used in the analysis include: *Gastrophryne carolinensis*, *Hyla cinerea* and *Lithobates sphenoccephalus*. Hydroperiod for the sampling frame in 2010 ranged from 336 to 365 days (mean \pm SD; 349 ± 7.74) and 32 of 60 cells (53%) including a study site were treated for exotics in the past three years (Table 3-3).

Effect of Survey Method

All three datasets (call, VES, combined) produced occupancy estimates [ψ (.)] that were equal to or higher than observed occupancy [ψ (obs)] (Table 3-4). Differences between predicted occupancy [ψ (.)] and observed occupancy [ψ (obs)] suggests that the combined dataset predicted occupancy equally or better than the call and VES datasets for all three species. Occupancy estimates produced by the call survey and combined datasets were equal for *H. cinerea*. Differences between occupancy estimates [ψ (.)] and observed occupancy [ψ (obs)] were greatest using the call survey dataset for both *G. carolinensis* and *L. sphenoccephalus*.

Estimates of detection probability varied drastically by species and sampling method (Table 3-4). Detection of *H. cinerea*, across all sampling methods, was significantly greater than the other two species. For *H. cinerea* call surveys were significantly better at detecting the species than VES. On the other hand, detection probabilities were higher using VES than call surveys for both *G. carolinensis* and *L. sphenoccephalus*, although both methods had moderately to extremely low detection probabilities. For all species, combining the two sampling methods resulted in higher detection probabilities, supporting the use of multiple method sampling.

Detection Probability

The best detection model for *G. carolinensis*, with 0.24 AIC weight, was day specific detection, $p(\text{day})$ (Appendix B). Detection probabilities ranged from 0.04 to 0.49, increasing later in the season (Figure 3-2). Survey specific detection was the second best model, with 0.13 AIC weight, but represents a similar idea as $p(\text{day})$, so only $p(\text{day})$ was used to examine occupancy of *G. carolinensis*. The clear best detection model for *H. cinerea*, with 0.82 AIC weight, was an interaction between rainfall and day, $p(\text{rain}*\text{day})$ (Appendix B). Detection of *H. cinerea* increased on rainy days as the season progressed, and decreased on non-rainy days as the season progressed (Figure 3-3). There was no clear best model for detection probability for *L. sphenoccephalus* (Appendix B). The top detection model, with 0.11 AIC weight, was $p(\text{survey})$ (Figure 3-4). Although day was not the top model for all three species, a conspicuous pattern was observed where the detection probability increased for all species later in the season (Figure 3-5).

Occupancy

The naïve site occupancy for *G. carolinensis* was 0.50, or 30 of 60 sites. Individuals were detected at 5 (8%), 6 (10%), and 22 (37%) sites on the first, second, and third surveys respectively. The top ranked model for *G. carolinensis*, carrying 0.28 AIC weight, had constant occupancy with detection varying by day (Table 3-5). Site occupancy was estimated to be 1

across the entire sampling frame (but see below). Models that included hydroperiod or treatment history appeared to be close competitors to the best model, with similar AIC values and within 2 Δ AIC from the top model. However, these results are spurious, as numerical convergence was never reached and the -2log-likelihoods (hereafter -2LL) of these models are all very similar to the top model (Anderson and Burnham 1998). This suggests that adding these variables did not substantially improve the modeling of the data. Even the best ranked model for *G. carolinensis* had confidence intervals that broadly overlapped zero. Moot occupancy estimates are likely a result of extremely low detection probability, so there was a low chance of observing the species even when it was present at a site. Future surveys that better account for detection should be conducted to confirm occupancy status of *G. carolinensis* in the Refuge, and improve precision of parameter estimates. Models that did not incorporate a detection variable did substantially worse than models that accounted for detection.

The naïve site occupancy for *H. cinerea* was 1.0, or 60 of 60 sites. Individuals were detected at 45 (75%), 50 (83%), and 53 (88%) sites on the first, second, and third surveys respectively. The clear best model for *H. cinerea* had constant occupancy with an interaction between rain and day influencing detection (Table 3-5). This model carried 0.53 AIC weight and had 2.7 times more support than the second best model. Occupancy equaled 1 across the entire sampling frame. Models that incorporated hydroperiod or treatment history had extremely high standard errors and confidence intervals that broadly overlapped zero, a result of constant occupancy across the entire range of both variables. Models that incorporated a detection variable did slightly better than models that assumed constant detection.

The naïve site occupancy for *L. sphenoccephalus* was 0.77, or 46 of 60 sites. Individuals were detected at 24 (40%), 20 (33%), and 31 (52%) sites on the first, second, and third surveys

respectively. The top ranked model, carrying 0.33 AIC weight, had constant occupancy with survey specific detection (Table 3-5). It is estimated that *L. sphenoccephalus* occupies 90% (S.E. = 0.08) of sites within the sampling frame. The second best model also included constant occupancy and produced a similar occupancy estimate (0.91 ± 0.08), supporting the fact that the probability of site occupancy is equal at all sites. Treatment history and hydroperiod were included in the third and fourth top models, with AIC weights of 0.19 and 0.14, respectively, however the slopes for these terms were relatively small with large standard errors (estimate \pm S.E. = -1.65 ± 3.0 for treatment history; -0.40 ± 0.7 for hydroperiod). With such large standard errors no statistical difference was found between sites with different hydroperiod values or between treated and untreated sites. Models that included the best detection variable did not rank substantially better than models that assumed constant detection probabilities.

CHAPTER 4 DISCUSSION

Prior to the development of a monitoring program, comprehensive inventories of species are necessary to establish baseline information on presence and distribution of populations (Dodd 2009). This study conducted the first thorough inventory of adult anurans in the interior of the Refuge and estimated site occupancy and detection probabilities for three species using the occupancy modeling framework of MacKenzie et al. (2002). Eight anuran species were documented using standard sampling techniques, and site occupancy estimates ranged from 90% to 100% for three modeled species. As has been shown in other studies (Bailey et al. 2004), use of two sampling methods resulted in higher detection probabilities than a single method. The top model in all three model sets had constant probability of occupancy paired with a single covariate for detection. Occupancy estimates produced by the top model were significantly higher than naïve estimates for two species (*G. carolinensis* and *L. sphenoccephalus*). This discrepancy is a direct result of detection rates that ranged from extremely low (0.06-0.34) to moderate (0.37-0.57), highlighting the importance of incorporating detection probabilities into study design rather than using unadjusted count data.

This issue of imperfect detection has long been recognized as a major source of error in field studies (MacKenzie et al. 2002, Thompson 1992) and wildlife monitoring programs (Yoccoz et al. 2001). Results from this study indicate that detection probabilities for most anurans in the Refuge are less than one, even for apparently abundant and common species such as *H. cinerea*, and agree with other studies that found that naïve occupancy values underestimate true occupancy status of wildlife populations (Bailey et al. 2004, MacKenzie and Nichols 2004). In the case of secretive/ cryptic or rare species, such as *G. carolinensis* in this study, naïve occupancy estimates may be as much as 50% lower than their respective occupancy estimates.

Inferences about changes in occupancy that are based on unadjusted data (e.g. naïve occupancy), will be negatively biased (MacKenzie et al. 2002) and have the potential to lead to unfounded management actions. In such situations, perceived changes in population status may simply be a result of the observers' ability to find the species (MacKenzie 2006) rather than true population change.

Variation in anuran detection probabilities has been attributed to many factors, including: (1) environmental conditions (Rice et al. 2005, Weir et al. 2005), (2) temporal variation in behavior (Bridges and Dorcas 2000, Cook et al. 2011), (3) observer bias (Waddle 2006, Weir et al. 2005), (4) sampling effort and/ or methodology (Shirose et al. 1997, Smith et al. 2006, de Solla et al. 2005), (5) location (Sewell et al. 2010), and (6) population size (Tanadini and Schmidt 2011). In the present study, temporal and observer-based variation in detection was controlled for in the study design and a subset of covariates was selected based on results of similar studies. Detection probabilities varied by sampling method and time of year for all three species modeled in this study. These results support findings of similar studies that have found that use of multiple detection methods improves parameter estimates (Bailey et al. 2004) and that detection probabilities increase in summer months (Rice et al. 2004, 2005). The absence of environmental covariates in the top models is a result of the single season sampling design of this study. Restricting sampling to summer months this study, in effect, controlled for environmental conditions (i.e. warmer and wetter) that were found to be important factors improving detection probabilities in related studies (Rice et al. 2004, 2005). That detection probabilities progressively increased over the summer sampling period, however, suggests that extending sampling into the fall may improve detection probabilities further and thus result in more precise parameter estimates for the three modeled species.

Dramatic differences in detection probability were observed between species; average detection probability of *H. cinerea* was nearly twice that of *L. sphenoccephalus* and 4.5 times greater than *G. carolinensis*. The high detection probability for *H. cinerea* was expected considering the generalist nature of the species (Meshaka et al. 2000), and the frequency and volume of their call. Rice et al. (2005) also detected *H. cinerea* in large numbers using both VES and call surveys across all habitats in the Everglades. The moderately low detection probabilities for *L. sphenoccephalus*, on the other hand, were somewhat surprising. The species is commonly considered to be the most abundant anuran in Florida (Bartlett and Bartlett 1999), and large numbers were detected by Rice et al. (2004, 2005) in both ENP and BICY. The moderately low detection probabilities for this species are likely a result of the fact that sampling did not include much of the species fall breeding season (Ryan and Winne 2001). Detection of *L. sphenoccephalus* was almost entirely by VES, with call survey detections on only a few occasions late in the season. Extending sampling into the fall breeding season would likely improve the likelihood of detecting the species using both VES and call surveys. Detection probabilities for *G. carolinensis* were the lowest throughout the study. Other studies in the southeast have reported similar results (Rice et al. 2004, Rice et al. 2005, Walls et al. 2011), with detection frequently being less than 0.15. Walls et al. (2011) tentatively suggested that variation in parameter estimates for *G. carolinensis* in Louisiana may be a result of heavy rainfall. The opportunistic and explosive breeding behavior of this species during heavy rainfall (Mitchell and Lannoo 2005) lends some support to this hypothesis, however, no significant effect of rainfall was found in this study. Although only speculative, the low detection probability for *G. carolinensis* in this study may be a result of sampling methodology. Ground cover was infrequently flipped in pursuit of animals during this study to avoid disturbing or damaging

Refuge habitats. Life history characteristics, such as a cryptic and secretive nature, and the fact that individuals were occasionally encountered under cover on tree islands suggests that detection probability for *G. carolinensis* would increase with more thorough sampling.

Addressing the issue of imperfect detection is a critical step in development of a sampling design for use in long term monitoring programs. Adequately accounting for variation in detection ensures accuracy of occupancy estimates, and hence, usefulness of inferences to managers. A primary objective of this study was to determine the relationship between anuran occupancy and hydroperiod in the Refuge. It was predicted that shorter hydroperiod sites would have lower occupancy than intermediate or longer hydroperiod sites. However, low variation in hydroperiod during the sampling period made it impossible to adequately address this question. Hydroperiod only varied by 29 days within the sampling frame during the 2010 SFWMD water year, and as a result occupancy of all three species was estimated to be between 90% and 100%, with the probability of site occupancy being equal for all sites. With such a low range in hydroperiod, sampling during this study sampled sites with similar hydroperiod.

Other studies that have attributed differences in anuran distribution (Babbitt et al. 2003), abundance (Van Buskirk 2005), or richness (Snodgrass et al. 2000) to hydroperiod have frequently conducted their studies in depressional or ephemeral wetlands. This distinction between temporary and permanent wetlands is critical when trying to understand relationships between biotic and abiotic factors and amphibian distribution and community structure (Wellborn et al. 1996). For example, length and timing of drying events in temporary wetlands may limit distribution of anurans with longer larval periods, whereas, a larger predator base found in longer more permanent wetlands may limit distribution and abundance of anurans more susceptible to predation. Such differences may explain why anuran assemblages in the

Everglades tend to be more depauperate than temporary wetlands in the region (Babbitt and Tanner 2000). Earlier work on the distribution and trophic interactions of larval anurans in the Refuge suggested that distribution and density of some species is nonrandom, varying predictably by habitat and in relation to predator density (Baber et al. 2005). The fitness tradeoffs (i.e. body size, developmental rate, activity) made by each species, in combination with physical factors such as hydrology, play important roles in determining the distribution and abundance of species across environmental gradients (Wellborn et al. 1996). Determining specific biotic and abiotic mechanisms responsible for shaping distributional patterns of the anuran assemblage in the Everglades, and their interaction with one another, should be an important objective for future research.

Another objective of this study was to determine the relationship between exotic species treatment history and anuran occupancy. Unfortunately, although species occupancy was reported as high across both treated and untreated sites, my ability to draw strong conclusions on the direct effects of treatment history of anuran occupancy was hindered by the ambiguity of the data. I was only able to use treatment history as a binary variable due to the general nature of Refuge databases and detection probabilities for two of the three observed species were extremely low. As mentioned above, when species are rarely observed it results in large confidence intervals, indicating less precise parameter estimates. Furthermore, it was not known with 100% certainty whether one of the study sites used in this study was directly impacted by exotic species management or not. With ambiguous treatment history data and low probability of detection for *G.carolinensis* and *L. sphenoccephalus* it would be unwise to conclude that exotic species treatment history is having no effect on anurans in the Refuge. To determine the true relationship between exotic species management and anuran occupancy in the Refuge, future

studies that directly address potential impacts are needed. For example, a Before-After Control-Impact (BACI) design would be much better suited to address this question than a large scale occupancy study. These findings agree with other studies (i.e. Bailey et al. 2004) that emphasize the importance of having a good sampling design that insures that research and management questions are adequately addressed, and that chosen sampling sites are representative of the entire area from which inferences are to be drawn.

Conclusions and Future Directions

Site occupancy has increasingly become a popular method for monitoring status of wildlife populations (Bailey et al. 2004, Brander et al. 2007, Kroll et al. 2008). Similar to others, I found the use of occupancy as a state variable to be a useful and efficient means to document the distribution and relative abundance of species across the landscape (Bailey et al. 2004). Using both VES and call surveys eight of the twelve native anuran species known from south Florida, and no exotic anurans, were detected in the Refuge interior. Occupancy of *H. cinerea*, *G. carolinensis*, and *L. sphenocephalus* was estimated to be extremely high across the center of the Refuge, and the inclusion of detection probabilities in the modeling framework greatly improved estimates. However, as with any field study, a few caveats were revealed during this study that I would like to discuss in closing in hopes of encouraging and improving future sampling efforts. First, single-species occupancy estimates are sensitive to abundant and rare species. The maximum likelihood framework of the MacKenzie et al. (2002) occupancy models doesn't perform well when data is near the boundaries of 1 or 0. MacKenzie et al. (2002) discuss this issue in their simulation study, stating that occupancy estimates should be interpreted with caution in cases where occupancy is estimated at 1 and detection is below 0.15. These conditions are similar to the results for *G. carolinensis* in the present study. In such cases it is difficult for the model to distinguish between a true absence at a site and a site where the species simply

wasn't detected. As stated previously, future survey efforts in the Refuge would benefit by better accounting for variation in detection probability for rarely observed species.

Second, the single-species single-season models used in this study do not allow for unexplained heterogeneity in detection probabilities between sites, only variation explained by included covariates. If unexplained heterogeneity in detection probabilities exists then occupancy estimates have the potential to be biased (Royle and Nichols 2003). Recent empirical work with amphibian populations suggests that variation in population size or abundance is common and has the potential to strongly affect detection probabilities (Tanadini and Schmidt 2011). This being the case, it is easy to perceive a situation where less abundant species may be overlooked or unaccounted for in monitoring programs that don't account for variation in detection resulting from population size. A number of studies have developed techniques to address this potential source of bias in monitoring studies (Royle and Nichols 2003, Tanadini and Schmidt 2011). Tanadini and Schmidt (2011) suggest using past population index in the form of count data obtained from surveys in previous years as a covariate for detection in subsequent surveys. Because counts of individuals at each site were recorded during this survey, future surveys in the Refuge can test the methods of Tanadini and Schmidt (2011) by using this data as a covariate for detection.

Lastly, the present study was conducted as a first effort to document the anuran community of the Refuge and determine whether factors such as hydroperiod and treatment history were influencing occupancy. This effort was associated with larger efforts to inventory anuran populations in the Everglades in the face of large scale restoration (Rice et al. 2004, 2005). Following the methodology of these efforts, to ensure comparability, this study used the single-species single-season occupancy models of MacKenzie et al. (2002). While this method was

useful in accomplishing the goals of this initial study, the single-species single-season model has certain limitations. Single-season models only offer a snapshot of the population at a single point in time. Gaining an understanding of long term trends in populations, and factors influencing changes in site occupancy (i.e. extinction and colonization) are of even more use to managers (MacKenzie et al. 2003). Recent advances on the MacKenzie et al. (2002) occupancy models have resulted in exciting improvements on standard single-species based monitoring programs. These advances utilize an approach similar to the MacKenzie et al. (2002) and Royle and Kery (2007) occupancy models, but extend the models to include multiple species or an assemblage of ecologically similar species (Dorazio and Royle 2005, Kery and Royle 2008). This approach produces estimates of occurrence, colonization, extinction, and detection for each species of an ecologically similar assemblage of species by sharing or borrowing observational data among species (MacKenzie et al. 2005). In many cases this method produces more precise parameter estimates than single-species models, particularly for species with low detection probabilities (e.g. *G. carolinensis* in this study) (MacKenzie et al. 2005). This method utilizes a hierarchical Bayesian approach to estimation using methods of Bayesian computation (Markov chain Monte Carlo) (Walls et al. 2011). By modeling multiple species under a single hierarchical framework managers will be better informed about the status of an entire assemblage of species rather than basing management decisions on individual species or populations (Walls et al. 2011). Current work is being done to apply these methods to a large scale amphibian model in the greater Everglades (Joint Ecosystem Modeling, www.jem.gov/). Once completed, this model will serve as an important tool for managers to evaluate the status of anurans across the Everglades landscape and their response to ecosystem restoration.

Table 3-1. Anurans observed using call and visual encounter surveys in Arthur R. Marshall Loxahatchee National Wildlife Refuge during summer 2010 and number of individuals observed during visual encounter surveys.

Common Name	Scientific Name	Count
Cricket Frog	<i>Acris gryllus</i>	449
Little Grass Frog	<i>Pseudacris ocularis</i>	1
Eastern Narrowmouth Toad	<i>Gastrophryne carolinensis</i>	26
Pig Frog	<i>Lithobates grylio</i>	164
Southern Leopard Frog	<i>Lithobates sphenoccephalus</i>	80
Green Treefrog	<i>Hyla cinerea</i>	91
Pinewoods Treefrog	<i>Hyla femoralis</i>	0
Southern Toad	<i>Anaxyrus terrestris</i>	1

Table 3-2. Detection of each species by visual encounter surveys and call surveys in Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010.

Species	VES	Call Survey
<i>Acris gryllus</i>	X	X
<i>Pseudacris ocularis</i>	X	X
<i>Gastrophryne carolinensis</i>	X	X
<i>Lithobates grylio</i>	X	X
<i>Lithobates sphenoccephalus</i>	X	X
<i>Hyla cinerea</i>	X	X
<i>Hyla femoralis</i>	.	X
<i>Anaxyrus terrestris</i>	X	.

Table 3-3. Variation in covariate data used in modeling anuran species occupancy and detection probability in Arthur R. Marshall Loxahatchee National Wildlife Refuge.

Variable	Mean	SD	Low	High	Range
Air Temperature (°C)	27.9	1.5	23	32	9
Humidity (%)	83.6	5.7	71	99	28
Vegetation Cover (%)	50.9	9.7	28.9	66.8	37.9
Hydroperiod (Days)	348.8	7.7	336	365	29

Table 3-4. Comparison of different sampling methods using parameter estimates from constant model, $\psi(\cdot)$ $p(\cdot)$: Call survey data only (Call), Visual encounter survey data only (VES), and combined Call survey and VES survey data (Combined).

Call			
Species	$\psi(\text{obs})$	$\psi(\cdot) [\pm\text{SE}]$	$p(\cdot) [\pm\text{SE}]$
<i>Gastrophryne carolinensis</i>	0.27	1 [0]	0.09 [0.02]
<i>Hyla cinerea</i>	1	1 [0]	0.66 [0.04]
<i>Lithobates sphenoccephalus</i>	0.13	1 [0]	0.04 [0.02]
VES			
Species	$\psi(\text{obs})$	$\psi(\cdot) [\pm\text{SE}]$	$p(\cdot) [\pm\text{SE}]$
<i>Gastrophryne carolinensis</i>	0.37	1 [0]	0.13 [0.02]
<i>Hyla cinerea</i>	0.8	1 [0]	0.41 [0.04]
<i>Lithobates sphenoccephalus</i>	0.77	0.99 [0.1]	0.39 [0.06]
Combined			
Species	$\psi(\text{min})$	$\psi(\cdot) [\pm\text{SE}]$	$p(\cdot) [\pm\text{SE}]$
<i>Gastrophryne carolinensis</i>	0.5	1 [0]	0.18 [0.03]
<i>Hyla cinerea</i>	1	1 [0]	0.82 [0.03]
<i>Lithobates sphenoccephalus</i>	0.77	0.91 [0.08]	0.46 [0.05]

Table 3-5. Summary of AIC model selection for top models for *Hyla cinerea*, *Gastrophryne carolinensis*, and *Lithobates sphenoccephalus*; Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010. Hydroperiod is represented by ‘HP’, and treatment history is represented by ‘Treatment’. † denotes models that did not converge.

Model	-2 log-likelihood	K	AIC	ΔAIC	w
<u><i>Hyla cinerea</i></u>					
$\psi(\cdot) p(\text{rain}*\text{day})$	154.93	5	164.93	0	0.53
$\psi(\text{HP}) p(\text{rain}*\text{day})$	154.93	6	166.93	2	0.19
$\psi(\text{Treatment}) p(\text{rain}*\text{day})$	154.93	6	166.93	2	0.19
$\psi(\text{HP}+\text{Treatment}) p(\text{rain}*\text{day})$	154.93	7	168.93	4	0.07
$\psi(\cdot) p(\cdot)$	168.48	2	172.48	7.55	0.01
<u><i>Gastrophryne carolinensis</i></u>					
$\psi(\cdot) p(\text{Day})$	152.99	3	158.99	0	0.28
$\psi(\text{HP}) p(\text{Day})$ †	151.06	4	159.06	0.07	0.27
$\psi(\text{HP}+\text{Treatment}) p(\text{Day})$ †	149.21	5	159.21	0.22	0.25
$\psi(\text{Treatment}) p(\text{Day})$ †	151.64	4	159.64	0.65	0.2
$\psi(\cdot) p(\cdot)$	171.51	2	175.51	16.52	0
<u><i>Lithobates sphenoccephalus</i></u>					
$\psi(\cdot) p(\text{Survey})$	238.94	4	246.94	0	0.33
$\psi(\cdot) p(\cdot)$	243.54	2	247.54	0.6	0.24
$\psi(\text{Treatment}) p(\text{Survey})$	238.05	5	248.05	1.11	0.19
$\psi(\text{HP}) p(\text{Survey})$	238.6	5	248.6	1.66	0.14
$\psi(\text{HP}+\text{Treatment}) p(\text{Survey})$ †	237.44	6	249.44	2.5	0.09

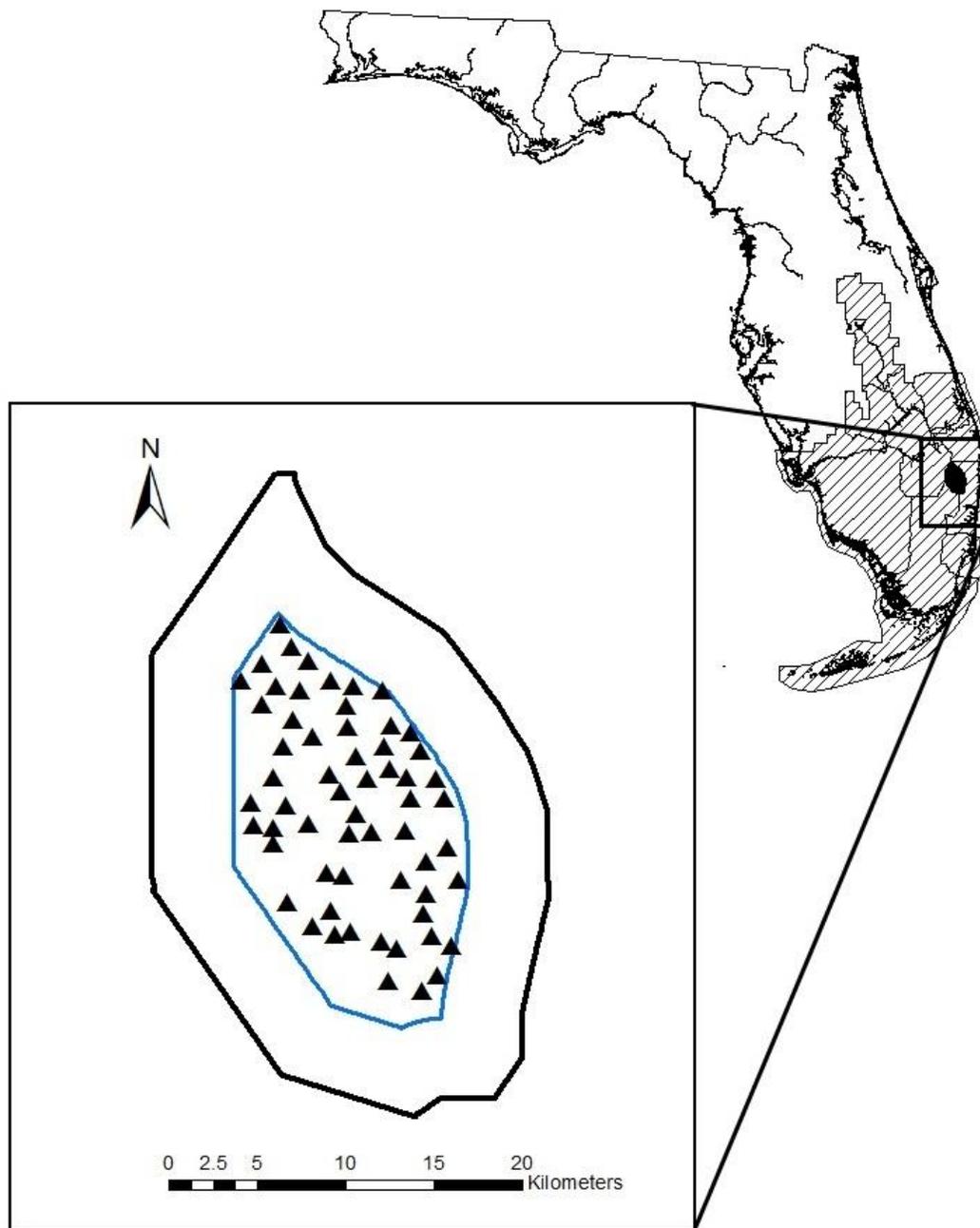


Figure 2-1. Location of Arthur R. Marshall Loxahatchee National Wildlife Refuge in Florida and location of study sites in the interior of the Refuge. Shaded area of south Florida represents the South Florida Water Management District Boundary. Triangles in the inset represent study sites and the blue line represents the sampling frame and is thus the area of inference used in this study.

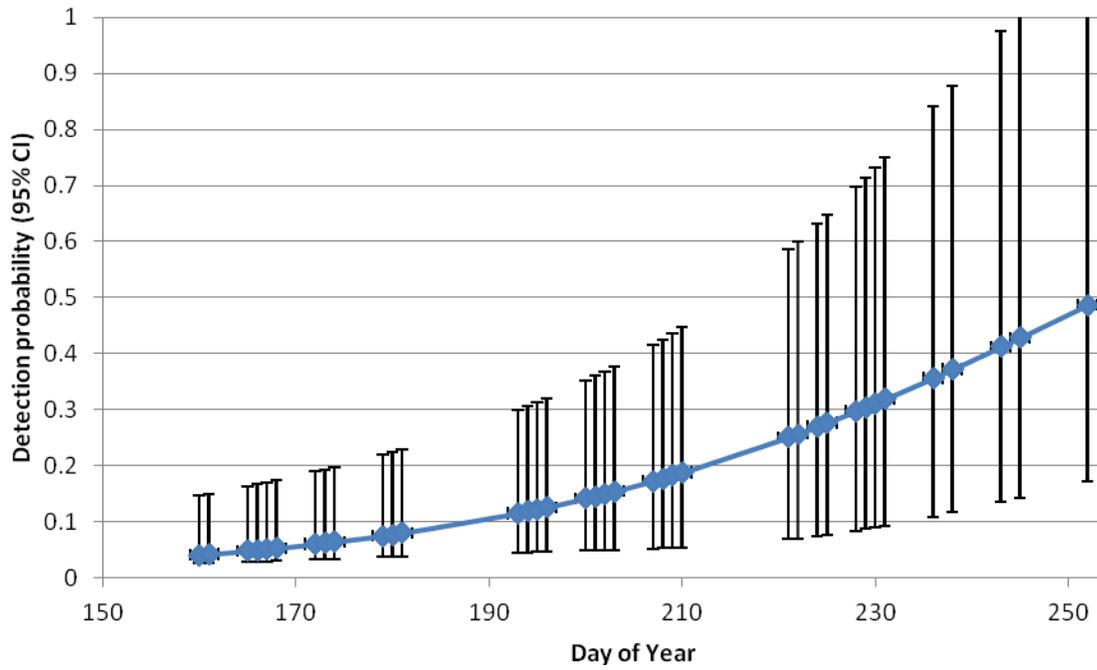


Figure 3-2. Relationship between detection probability and day of year for *Gastrophryne carolinensis* in Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010.

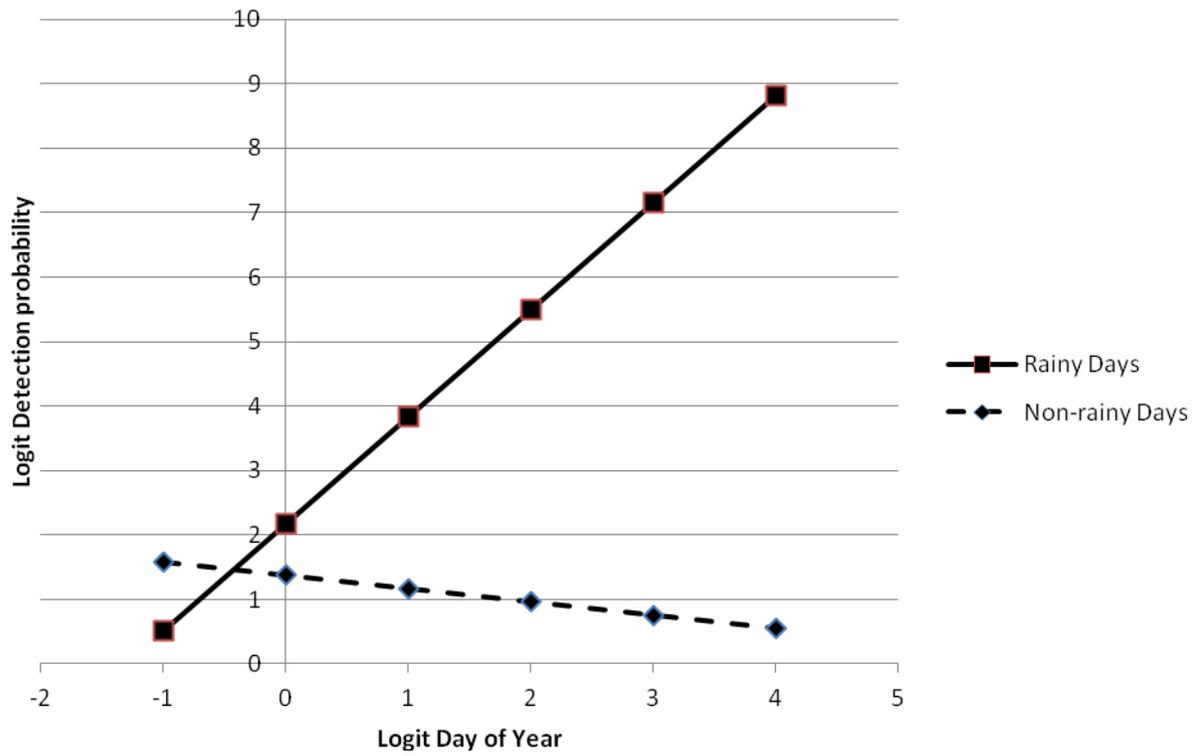


Figure 3-3. Relationship between detection probability and rain*day for *Hyla cinerea* in Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010.

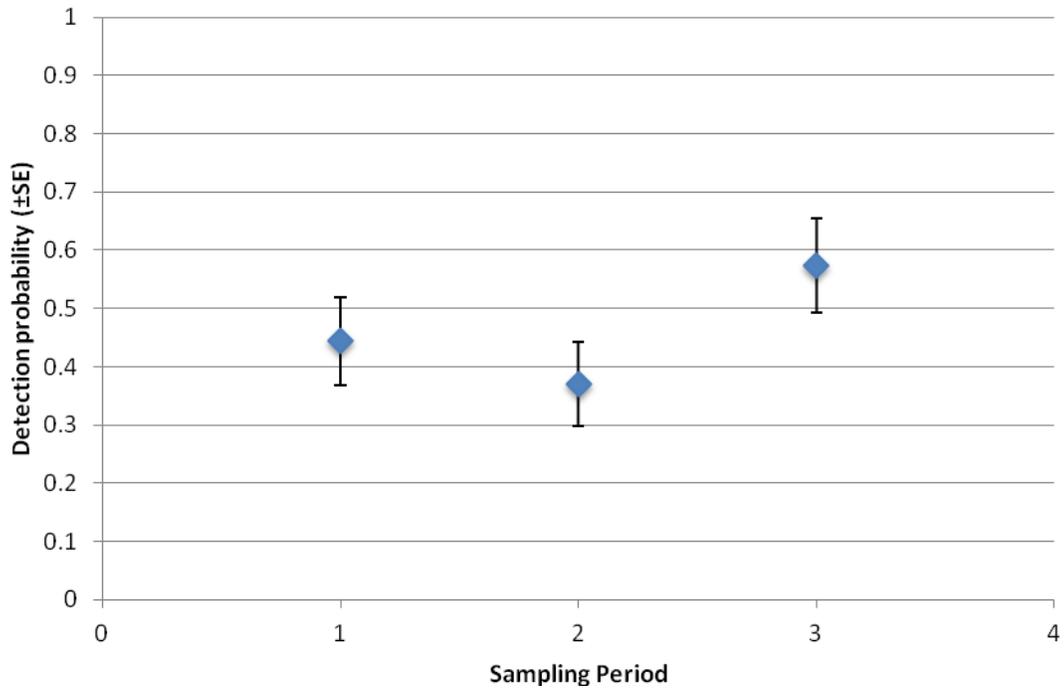


Figure 3-4. Relationship between detection probability and sampling period for *Lithobates sphenoccephalus* in Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010. Sampling period 1 was in June, sampling period 2 in July, and sampling period 3 in August.

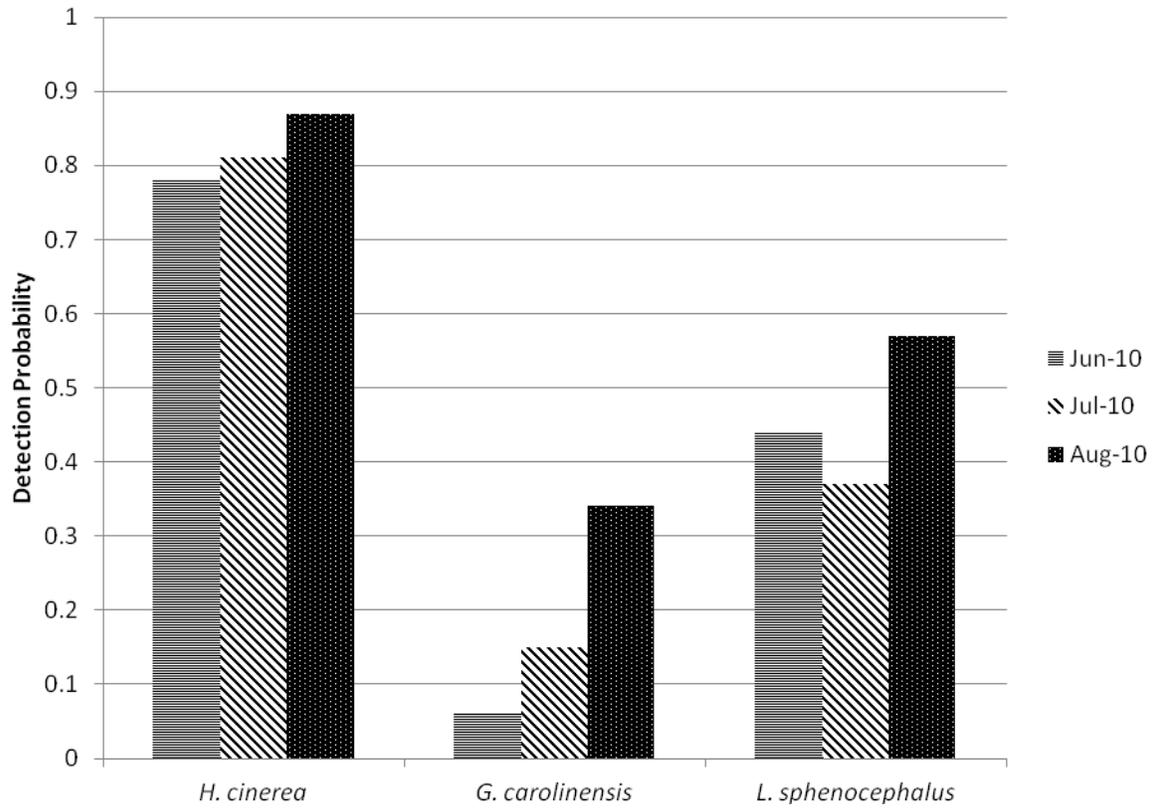


Figure 3-5. Average detection probability by sampling period for *Hyla cinerea*, *Gastrophryne carolinensis*, and *Lithobates sphenoccephalus* in Arthur R. Marshall Loxahatchee National Wildlife Refuge, summer 2010.

APPENDIX A
DETECTION MODELS

Table A-1. Detection models run for each anuran species in the first step of the modeling process. Variables were chosen because of their perceived influence on either anuran activity or observers ability to detect individuals.

Occupancy	Detection
$\psi(.)$	$p(.)$
$\psi(.)$	$p(\text{air temp.})$
$\psi(.)$	$p(\text{humidity})$
$\psi(.)$	$p(\text{veg. density})$
$\psi(.)$	$p(\text{rain})$
$\psi(.)$	$p(\text{day})$
$\psi(.)$	$p(\text{day} + \text{day}^2)$
$\psi(.)$	$p(\text{air temp.} + \text{rain})$
$\psi(.)$	$p(\text{air temp.} + \text{humidity})$
$\psi(.)$	$p(\text{air temp.} + \text{veg})$
$\psi(.)$	$p(\text{air temp.} + \text{day})$
$\psi(.)$	$p(\text{veg. density} + \text{rain})$
$\psi(.)$	$p(\text{veg. density} + \text{day})$
$\psi(.)$	$p(\text{rain} + \text{day})$
$\psi(.)$	$p(\text{air temp.} + \text{humidity} + \text{rain})$
$\psi(.)$	$p(\text{air temp.} + \text{veg. density} + \text{rain})$
$\psi(.)$	$p(\text{air temp.} + \text{rain} + \text{day})$
$\psi(.)$	$p(\text{air temp.} + \text{humidity} + \text{veg. density})$
$\psi(.)$	$p(\text{veg. density} + \text{rain} + \text{day})$
$\psi(.)$	$p(\text{air temp.} * \text{veg. density})$
$\psi(.)$	$p(\text{air temp.} * \text{day})$
$\psi(.)$	$p(\text{rain} * \text{day})$

APPENDIX B
DETECTION MODEL RESULTS

Table B-1. Summary of AIC model selection for all detection models run in the first step of the modeling process. Top model for each species that was used in the final model set is set in bold and model weights are in parentheses.

		AIC values (model weight)		
Occupancy	Detection	<i>G. carolinensis</i>	<i>H. cinerea</i>	<i>L. sphenoccephalus</i>
$\psi(\cdot)$	$p(\cdot)$	175.51 (0.00)	172.48 (0.02)	247.54 (0.08)
$\psi(\cdot)$	$p(\text{day})$	158.99 (0.24)	173.42 (0.01)	247.19 (0.10)
$\psi(\cdot)$	$p(\text{humidity})$	175.9 (0.00)	173.6 (0.01)	248.88 (0.04)
$\psi(\cdot)$	$p(\text{air temp.})$	176.7 (0.00)	174.41 (0.01)	249.52 (0.03)
$\psi(\cdot)$	$p(\text{rain})$	175.85 (0.00)	173.37 (0.01)	249.48 (0.03)
$\psi(\cdot)$	$p(\text{survey})$	160.29 (0.13)	172.78 (0.02)	246.94 (0.11)
$\psi(\cdot)$	$p(\text{veg. density})$	176.86 (0.00)	172.62 (0.02)	247.71 (0.08)
$\psi(\cdot)$	$p(\text{day} + \text{day}^2)$	160.77 (0.10)	174.51 (0.01)	247.52 (0.08)
$\psi(\cdot)$	$p(\text{air temp.} + \text{day})$	160.98 (0.09)	175.42 (0.00)	248.87 (0.04)
$\psi(\cdot)$	$p(\text{air temp.} + \text{humidity})$	176.19 (0.00)	175.59 (0.00)	250.88 (0.01)
$\psi(\cdot)$	$p(\text{air temp.} + \text{rain})$	175.92 (0.00)	174.95 (0.01)	251.43 (0.01)
$\psi(\cdot)$	$p(\text{air temp.} + \text{veg. density})$	178.01 (0.00)	174.56 (0.01)	249.65 (0.03)
$\psi(\cdot)$	$p(\text{rain} + \text{day})$	160.78 (0.10)	174.68 (0.01)	248.83 (0.04)
$\psi(\cdot)$	$p(\text{veg. density} + \text{day})$	160.3 (0.13)	173.52 (0.01)	247.34 (0.09)
$\psi(\cdot)$	$p(\text{veg. density} + \text{rain})$	177.35 (0.00)	173.27 (0.01)	249.7 (0.03)
$\psi(\cdot)$	$p(\text{veg. density} + \text{rain} + \text{day})$	162.08 (0.05)	174.53 (0.01)	249.15 (0.03)
$\psi(\cdot)$	$p(\text{air temp.} + \text{humidity} + \text{rain})$	175.98 (0.00)	175.77 (0.00)	252.7 (0.01)
$\psi(\cdot)$	$p(\text{air temp.} + \text{humidity} + \text{veg. density})$	177.6 (0.00)	175.75 (0.00)	251 (0.01)
$\psi(\cdot)$	$p(\text{air temp.} + \text{rain} + \text{day})$	162.68 (0.04)	176.55 (0.00)	250.06 (0.02)
$\psi(\cdot)$	$p(\text{air temp.} + \text{veg. density} + \text{rain})$	177.42 (0.00)	174.82 (0.01)	251.62 (0.01)
$\psi(\cdot)$	$p(\text{air temp.} * \text{day})$	162.71 (0.04)	176.55 (0.00)	250.75 (0.02)
$\psi(\cdot)$	$p(\text{air temp.} * \text{veg. density})$	177.35 (0.00)	176.45 (0.00)	249.31 (0.03)
$\psi(\cdot)$	$p(\text{rain} * \text{day})$	160.86 (0.10)	164.93 (0.82)	247.13 (0.10)

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BIOGRAPHICAL SKETCH

Ryan Lynch was born in Palo Alto, California, in 1981. Ryan spent most of his childhood in the San Francisco Bay Area, specifically in a small corner of the city of Fremont known as Niles. He received his high school diploma from Washington High School in 2000. Following high school Ryan attended Eckerd College in St. Petersburg, Florida, where he received a Bachelor of Arts degree in anthropology, biology and environmental studies in 2004. During his college career Ryan worked on a number of research projects, including a long term turtle population study in north Florida, a hermit crab behavioral study in Costa Rica, and a semester long wildlife program in Kenya. After receiving his degree, Ryan moved to Ecuador to pursue an assistant research position at a biological research station on the eastern slope of the Andes. In 2006, Ryan returned to Florida to work for the University of Florida as a technician on an exotic fern project. During the next three years Ryan also assisted with an assortment of herpetological projects, including work with alligators, crocodiles, and the exotic Burmese pythons. In late 2008, Ryan enrolled at the University of Florida to pursue a Master of Science degree in the School of Natural Resources and Environment.